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Torrey Botanical Club

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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 85, NO. 6, PP. 397–404 DECEMBER, 1958

A STUDY OF THE NATURE OF INTRASPECIFIC AVERSION IN DIPLODIA MAYDIS[1]

A. J. ULLSTRUP[2]

Intraspecific aversion in *Diplodia maydis* (Berk.) Sacc. = (*D. zeae* (Schw.) Lev.) (Conners 1956) is clearly observed in pure culture when two colonies of opposite reaction type approach each other on a solid agar substrate. At the interface of two averting colonies growth of each ceases and a line of demarcation is formed, characterized by reduced aerial mycelium and a darkening of the substrate (fig. 1). Compatibility between cultures is characterized by a piling up or "drifting" of the mycelium, and the absence of a dark line in the substrate at the juncture of the two colonies (fig. 1). When a random collection of isolates is plated on an agar substrate in all possible pairings, the great majority of such pairs show aversion. All subcultures of a single isolate are compatible with each other.

The present paper reports preliminary studies designed to obtain some understanding of the nature of aversion in *D. maydis*.

Aversion in *D. maydis* was first described by Hoppe (1936); similar phenomena have been observed in *Fomes pinicola* (Fr.) Cooke (Mounce 1929), in *Diaporthe perniciosa* Marchal (Cayley 1923), and in *Corticium calceum* F. (Brodie 1935). Nakata (1927) concluded that aversion in *Sclerotium rolfsii* Sacc. was due to the secretion of a toxic substance by the mycelia of averting cultures, and was independent of the medium on which the fungus was grown. Dimond (1939) in a study of aversion in *D. maydis* worked primarily with single cultures and found no marked difference in the physiology of averting cultures. She was not able to isolate a toxic substance.

Methods and materials. Cultures of *D. maydis* were isolated by plating corn kernels infected with the fungus on acidified potato-dextrose agar. Sub-cultures from these platings were paired on potato-dextrose agar to determine their aversion reaction, and appropriate cultures were then selected. In the preparation of filtrates, broth was seeded with spore suspensions of averting cultures in the same vessel in order to provide for the interaction of a very large number of small colonies. Spores were produced

[1] Contribution from the Department of Botany and Plant Pathology, Purdue University, Lafayette, Indiana, and Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture. Journal Paper No. *1242* of the Purdue Agricultural Experiment Station.

[2] Pathologist, Department of Botany and Plant Pathology, Purdue University, and Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture.

[THE BULLETIN for September–October 1958 (85: 313–396) was issued November 12, 1958]

by growing single cultures on moist sterilized whole oats in 125 ml. erlenmeyer flasks for 4 to 6 weeks at 22° to 25° C. in constant light. Suspensions were made by adding sterile water to flasks in which mature pycnidia were

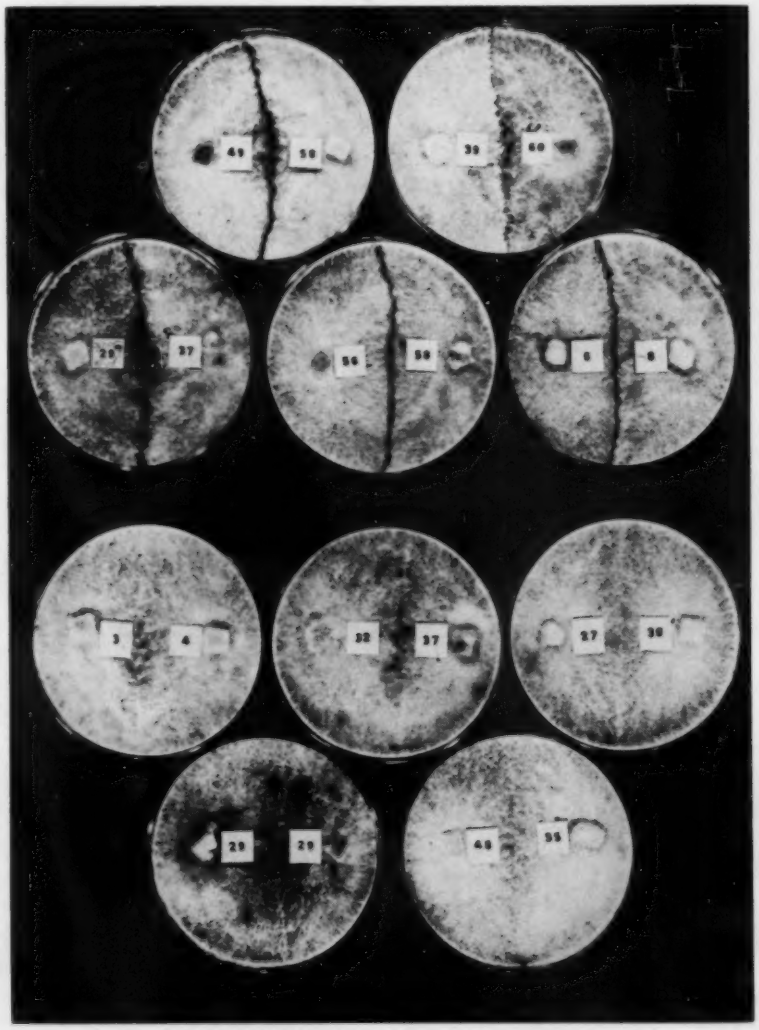

FIG. 1. Aversion and compatibility in *Diplodia maydis*. Upper 5 plates show typical aversion between pairs of cultures. Lower 5 plates are seeded with compatible pairs of cultures.

present and shaking until the water was dark with suspended spores. Where simultaneous seedings of paired cultures were made, equal quantities of suspension from appropriate cultures were mixed.

Potato-dextrose broth[3], used exclusively to produce filtrates, was dispensed in 1-liter or 2-liter flasks, or in 2-quart flat-sided milk bottles. The depth of broth in these vessels ranged from 2 to 3 cm.

Filtrates were extracted 3 times with 1/10 volume of chloroform in a separatory funnel. This extraction was essentially complete; the second and third extractions were low in activity and the aqueous fraction showed little toxicity. The three chloroform extractions were combined and the chloroform removed under vacuum at 60° C. The amorphous residue was taken up in fresh potato-dextrose broth to test the activity of chloroform extracts.

Experimental. Preliminary studies had shown that when a pair of averting cultures was seeded simultaneously in potato-dextrose broth and incubated 12 to 20 days, the collected filtrate inhibited completely the growth

TABLE 1. *Dry weights of mycelial mats of a culture of Diplodia maydis when grown for ten days on filtrates produced by averting culture pairs and by compatible culture pairs. Each figure for dry weight is the average of 3 mycelial mats.*

Culture Combination (Averting Pairs)	Age of filtrate when harvested (Days)	Dry weight of mycelial mats when grown on filtrates (mg.)	Culture Combination (Compatible Pairs)	Age of filtrate when harvested (Days)	Dry weight of mycelium when grown on filtrates (mg.)
6 + 8	8	80	3 + 4	8	110
	10	0		10	100
	12	0		12	94
	20	0		20	76
56 + 58	8	101	27 + 30	8	130
	10	36		10	102
	12	0		12	95
	20	0		20	71
49 + 58	8	105	32 + 37	8	105
	10	95		10	104
	12	0		12	102
	20	0		20	60

of any culture of *D. maydis*. The filtrates produced by these cultures grown separately were not toxic.

An experiment was set up to determine the relation of length of incubation period to the production of the toxic material in the filtrates. Three averting pairs of cultures were seeded in potato-dextrose broth and filtrates of each harvester after 8, 10, 12 and 20 days. Filtrates were dispensed in 25 ml. amounts in 125 ml. flasks, autoclaved, reseeded with a single culture of *D. maydis*, incubated 10 days, and mycelial mats harvested and dry weights determined. For comparison, three compatible pairs of cultures were seeded in potato-dextrose broth and filtrates harvested and seeded in a similar manner. The data in Table 1 indicate that the toxic substance is

[3] 200 gms. of peeled, sliced potatos steamed for ½ hr., filtered through cheesecloth; 20 gms. of dextrose dissolved in the broth and then autoclaved 20 minutes at 15 pounds pressure.

produced in sufficient quantity to be completely inhibitory after an incubation period of between 10 or 12 days. These data also suggest some difference between averting culture pairs with respect to the rapidity of production of the toxic principle. The data on the filtrates produced by compatible culture pairs showed no marked inhibition of growth when reseeded. There was a decline in the weights of mycelial mats from the 8th to the 20th day of incubation but this reduction may be attributed to depletion of nutrients rather than the production of a specific toxic material.

It was observed that the mycelial mats produced by combined averting cultures were thinner, darker in color, and possessed appreciably less aerial mycelium than those produced by compatible culture pairs or by single cultures. An averting culture pair, 6 + 8, was seed in 12 flasks of potato-

TABLE 2. *Dry weights of mycelial mats produced on potato-dextrose broth by an averting pair of cultures and by a compatible pair of cultures when incubated for different periods at 22° to 25° C. Each figure for dry weight is the average of 2 mycelial mats.*

Culture Combination	Days to Harvest	Dry Weight of Mycelial Mats
Averting pair	days	mg.
6 + 8	8	43
	10	44
	12	43
	14	45
	16	44
	18	46
Compatible pair		
3 + 4	8	77
	10	137
	12	165
	14	227
	16	193
	18	231

dextrose broth and incubated at 22°–25° C. Mycelial mats were harvested 2 at a time, and dry weight determined 8 days after seeding and thereafter at 2-day intervals until the 18th day. The same procedure was followed using a pair of compatible cultures, 3 + 4. The data in Table 2 show that the growth of mycelial mats produced by the averting culture pair remained essentially stationary after the 8th day of incubation. Mycelial growth of the compatible culture pair increased generally over the incubation period. It appears from these data that when averting cultures are combined in pairs the toxic material(s) reaches a concentration, after about 8 days of incubation, that is sufficient to suppress further growth of mycelium.

When single members of an averting pair of cultures were grown in separate flasks of broth and the filtrates mixed in equal proportions, no toxicity was evident when such combined filtrates were reseeded.

Toxic filtrates developed only in stationary culture. Filtrates produced in shake flasks, or in which the medium was agitated by means of a stream of sterile air or by a mechanical stirrer, were non-toxic.

To determine if fungi other than *D. maydis* were affected by the toxic material produced in filtrates on which averting pairs of isolates had grown, the following experiment was undertaken. Flasks containing sterile potato-dextrose broth were seeded with equal volumes of spore suspensions of isolate 29 and of isolate 39. These two isolates showed marked aversion on potato-dextrose agar. Another lot of flasks containing the same broth was seeded with a suspension of spores derived from isolate 27 and from isolate 30. These two isolates were compatible. After 15 days of incubation at 24° C. the filtrates were harvested, dispensed in 25 ml. amounts in 125 ml.

TABLE 3. *Growth of various test fungi, when seeded on 15-day old filtrates derived from a compatible (27–30) pair and from averting (29–39) pair of isolates of D. maydis. Each figure for dry weight is the average of 2 mycelial mats.*

Test Fungus	Dry weight of mycelium	
	Filtrate	
	27–30 (compatible)	29–39 (averting)
	mg.	mg.
Aspergillus niger	12	6
Rhizopus nigricans	6	4
Penicillium oxalicum	11	3
Fusarium moniliforme	13	1
Nigrospora oryzae	30	no growth
Gibberella zeae	11	" "
Diplodia maydis	22	" "
Botrytiscinerea	45	" "
Rhizoctonia solani	10	" "
Helminthosporium turcicum	2	" "

erlenmeyer flasks, and autoclaved. Two flasks were seeded with each fungus species to be tested. Ten days after incubation at 24° C. the mats were harvested, dried and weighed. The data in table 3 shows that all of the fungi tested were inhibited by the toxic material produced in filtrates on which the averting pair of isolates had grown, and that some were much more affected than others.

The H-ion concentration of the filtrates varied with different experiments, with the incubation period, and with culture or culture combination used to seed the broth. In general, filtrates on which averting culture pairs had grown were somewhat more acid than those on which compatible pairs or single cultures had grown. The H-ion concentration of filtrates in different experiments ranged from about pH 4.2 to pH 6.8, which is within the range at which *D. maydis* will grow. To determine if H-ion concentration of the filtrates from averting pairs of cultures was responsible for the toxic effects, a portion of a 10-day-old filtrate was adjusted from pH 4.2

to pH 5.5 before seeding. A similar portion of a 10-day-old filtrate from a compatible pair of cultures of pH 6.3 at the time of harvest was adjusted to pH 4.0 and seeded. No growth took place on the filtrate from the averting culture pair at pH 4.2 or after adjusting to pH 5.5. The filtrate from a compatible culture pair at pH 6.3 produced an average of 51.2 mg. of dry wt. of mycelium 10 days after seeding. The same filtrate adjusted to pH 4.0 produced 51.5 mg. of dry weight of mycelium 10 days after seed-

TABLE 4. *Dry weights of mycelial mats produced on filtrates and filtrate fractions when reseeded with a culture of Diplodia maydis.*

Culture pair or single cultures used to seed original broth.	Culture numbers	Filtrate fraction	Dry weight of mycelial mats (Av. of 3 mats)
			mg.
Averting pairs	6 + 8	Unextracted filtrate	0
		Chloroform fraction	0
		Aqueous fraction	125
	29 + 37	Unextracted filtrate	0
		Chloroform fraction	0
		Aqueous fraction	78
Compatible pairs	3 + 4	Unextracted filtrate	237
		Chloroform fraction	180
		Aqueous fraction	225
	32 + 37	Unextracted filtrate	141
		Chloroform fraction	178
		Aqueous fraction	150
Single cultures	6	Unextracted filtrate	162
		Chloroform fraction	218
		Aqueous fraction	173
	8	Unextracted filtrate	147
		Chloroform fraction	139
		Aqueous fraction	124
	3	Unextracted filtrate	160
		Chloroform fraction	143
		Aqueous fraction	184
	4	Unextracted filtrate	114
		Chloroform fraction	168
		Aqueous fraction	170

ing. These results suggest that the toxicity of filtrates is not due to their H-ion concentration.

Extraction of the toxic material from filtrates. Solvents used in a preliminary attempt to extract the toxic material from filtrates produced by combined averting cultures of *D. maydis* were ethyl ether, ethyl acetate, petroleum ether and chloroform. Only the latter appeared to be effective. Extractions were carried out as described above. The amorphous residue of

the chloroform fraction extracted from each 100 ml. of filtrate was taken up in 100 ml. of fresh potato-dextrose broth; this was divided into four 25 ml. amounts in 125 ml. flasks and autoclaved. The aqueous fraction, which was heated for 10 minutes at 60° C. to remove any residual chloroform, and the unextracted filtrate were also divided into 25 ml. amounts and autoclaved. The same procedure was followed with filtrates produced by combined compatible cultures and by single cultures. After autoclaving, all media, the unextracted filtrate, the aqueous fraction, and the residue from the chloroform fraction taken up in fresh potato-dextrose broth, were seeded with a spore suspension of a culture of *D. maydis*. After 10 days' incubation at 22°–25° C., mycelial mats were harvested, dried and weighed.

The data in Table 4 indicate the effectiveness of chloroform in the toxic principle from the filtrates produced by combined averting cultures. The apparent absence of toxic material in filtrates produced by combined compatible cultures and by single cultures is also shown.

Discussion. The results of the studies reported in this paper suggest that aversion in *D. maydis* is a type of antibiosis. It differs from the general concept of antibiotic activity in which a single species or strain of an organism produces a by-product toxic to certain other organisms, in that two cultures of the same species are required for production of the toxic material. Both members of an averting pair are sensitive to the toxin.

The mechanisms by which the toxin is produced or the stimuli responsible for its production when two averting cultures come into contact with each other are unknown. In approximately 100 random isolates paired in all possible combinations, about 85% of such pairings showed aversion. Further work with much larger numbers of cultures is necessary to determine more accurately the ratio of aversion to compatibility when random isolates are paired.

SUMMARY

1. Averting pairs of cultures of *D. maydis* when seeded simultaneously in potato-dextrose broth and incubated for 10 to 20 days at a temperature ranging between 22° to 25° C., produced filtrates that were toxic to cultures of the same species and to a number of other fungi. Toxicity of filtrates appeared not to be due to H-ion concentration. Toxic filtrates were produced only in stationary culture. Filtrates from shake cultures, or from those in which the medium was agitated with a stream of sterile air or by a mechanical stirrer, were non-toxic. Filtrates produced by single cultures were not toxic. When two such filtrates were combined in equal volume the resulting mixture was non-toxic, even though the cultures produced a toxin when incubated together. Comparable filtrates produced by paired compatible cultures were not toxic.

2. The maximum dry weight of mycelial mats produced by paired averting cultures was attained about 8 days after seeding the broth and then remained constant for the remainder of the incubation period (18 days). The dry weight of mycelial mats harvested from paired compatible cultures increased steadily over the incubation period and, at the termination of the experiment, exceeded by five times the dry weight of mats of the paired averting cultures.

3. Chloroform was effective in extracting the toxic material from filtrates of paired averting cultures, but ethyl ether, ethyl acetate and petroleum ether were not effective.

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CYTOTAXONOMIC STUDIES IN THE LEGUMINOSAE[1]

C. A. BERGER, E. R. WITKUS AND R. M. MCMAHON

The occurrence of polyploid cells and divisions in diploid species of plants has been reported since the 1916 publications of Winkler. More recently it has been observed that the formation and division of these polyploid cells occur at a definite time and place in development and constitute part of a developmental pattern that is highly specific. This was found to be true of a number of leguminous plants. Ghimpu (1929) studied polyploidy in certain Leguminosae and observed cells with diploid and tetraploid numbers of chromosomes in races of some African and Asiatic species of *Acacia*. Senn (1938) in his study on chromosome number relationships in the Leguminosae reported somatic doubling in root tip cells of *Cassia nictitans* and *Albizzia julibrissin*. In *Cassia nictitans* the number of such doubled cells increased with the distance from the tip of the root. His statements indicate that all these divisions showed the paired association of chromosomes. In the polyploid divisions in *Albizzia julibrissin* the pairing of the chromosomes was not as evident as in *Cassia nictitans*. Jacob (1940) noted the presence of an occasional tetraploid division in the cells of the root tip of *Cassia Tora* and *Poinciana* (*Delonyx*) *regia*. Witkus and Berger (1947) demonstrated the presence of polyploid divisions at a definite time and place in the development of *Mimosa pudica*. Mitoses first appeared in the root tips of seedlings 2 mm. in length. Figures 1 and 2 are photomicrographs of diploid metaphases. Tetraploid divisions were abundant at the beginning of the mitotic activity in the root meristem. The frequency of the 4n divisions was observed to increase to a maximum in seedlings of 4 mm. lengths and then to decrease with further increase in the length of the germinating seedling. In seedlings 10 mm. long or longer only an occasional polyploid division was noted. There was no evidence of any degree of polyploidy other than tetraploidy. All the polyploid divisions showed the paired arrangement of the chromosomes at prophase and metaphase (figs. 3–5). Since these tetraploid divisions were found in the roots of very young seedlings (2 mm. in length), the authors concluded that the polyploid condition probably arose during the early embryology of the plant. Tjio (1948) reported the presence of tetraploid and octoploid divisions in the primary root meristem of *Mimosa invisa* and *Mimosa pudica*. Some of these divisions showed the paired association of chromosomes; while others showed the unpaired association of chromosomes. Tjio (1948) also reported the pres-

[1] This investigation was aided by a Grant (G2235) from the National Science Foundation.

ence of polyploid divisions in the root meristem of *Acacia retinodes* and *Leucaena glauca*. The tetraploid divisions in *Leucaena glauca* showed the paired arrangement of chromosomes. No polyploid divisions were observed in the meristematic regions of secondary roots. In *Albizzia julibrissin* Durazz, Berger and Witkus (1950) found polyploid mitoses in the root tips of young seedlings from 2 mm. to 30 mm. in length. The frequency of the polyploid divisions increased to a maximum in a 5 mm. seedling and then decreased. The degree of polyploidy, with rare exceptions, was tetraploid. The tetraploid divisions were found in dermatogen as well as periblem cells. Both paired and unpaired metaphases were observed, indicating that some of the polyploid cells had undergone more than one division before they became differentiated. Two types of paired metaphases were noted, one with normal length chromosomes and ones with supercontracted chromosomes. Figures 6 to 9 are photomicrographs of the different types of divisions.

LaFleur (1953) observed polyploidy in the periblem of root tips of *Delonyx regia*. The maximum number of 4n divisions was found in the 4 mm. seedlings. The number of such divisions decreased as the seedlings increased in length. Polyploidy was restricted to the cells of the periblem and no degree of polyploidy higher than tetraploidy was observed.

Moraski (1953) reported polyploid divisions as being very abundant in young germinating seedlings of *Cassia marilandica*. The divisions were all tetraploid and occurred in the region of the periblem of the root meristem. Again it was observed that the maximum number of divisions was noted in the 4 mm. seedlings and after this length there was a steady decrease in the frequency of the polyploid divisions. No octoploid divisions were noted. Figures 10 and 11 are photomicrographs of the different types of divisions found in the root meristem.

Power (1955) studied the cytological development of *Schrankia uncinata*. He reported polyploid divisions in the periblem layer of the root tips of young seedlings, ranging from 2 mm. to 20 mm. in length. Both tetraploid and octoploid divisions were found. Paired and unpaired divisions were observed. As in *Albissia julibrissin* two types of paired metaphases were noted, one with normal length chromosomes and ones with supercontracted chromosomes. The polyploid divisions were most abundant in very young seedlings and decreased in number as the seedlings increased in length (figs. 12–14). An occasional polyploid division was found in the secondary roots.

Laurencot (1955) reported polyploid divisions in the seedlings of *Acacia catechu* early in development. Tetraploid divisions with paired and unpaired chromosomes were noted. As previously reported for *Albizzia julibrissin* two types of paired metaphases were noted, one with normal length

chromosomes and one with supercontracted chromosomes. These divisions are shown in figures 15 to 18.

These studies indicated that naturally occurring polyploidy in the development of diploid species may be widespread in leguminous plants. An intensive study of the family Leguminosae was accordingly undertaken including representative genera from each of the subfamilies. This study was also made to determine if the phenomenon is universally present in the legumes or restricted to a particular subfamily.

Material and methods. Seventy-nine species from fifty-five genera representative of the three subfamilies of the family were studied. Many of these plants are now under cultivation in the Fordham Biology Department Greenhouse.[2] Seeds were allowed to germinate on moist filter paper in Petri dishes until they reached the required length. The root tips were then placed in Craf fixative. Using standard procedures cross sections cut at eight microns were prepared of each of the roots. Seedlings were cut when they were 2, 4, 6, 8, 10, 12, 14, 20 and 30 mm. long. The number of seedlings of each length studied depended upon the availability of the seeds. To facilitate germination, the seed coats of some of the larger seeds were pierced. In the case of *Cercis chinensis* germination was greatly enhanced by immersing the seeds in a 0.1% solution of gibberellin for twenty-four hours. The sections were stained using the standard iron alum hematoxylin staining technique. Table 1 is a list of the plants studied. The chromosome numbers given are those listed in "Chromosome Atlas of Flowering Plants" by Darlington and Wylie with the exception of some species of *Aeschynomene* which were determined in the present investigation. The source of each seed is also given.

Observations and results. Subfamily Mimosoideae. In the subfamily Mimosoideae, in all species studied with one exception polyploid divisions were abundant at the beginning of the mitotic activity in the root meristem (figs. 19 to 32). The frequency of 4n divisions was observed to increase to a maximum in seedlings 4 to 6 mm. in length and then to decrease in number with the increase in the length of the germinating seedling. Most of the polyploid divisions were tetraploid. Generally both paired and unpaired divisions occurred. The pairing was most evident in prophase. In *Schrankia uncinata, Acacia catechu, Albizzia julibrissin* and *Leucaena tricodes* two types of paired metaphases were noted, one with normal length chromosomes and ones with supercontracted chromosomes (figs. 8, 9, 17 and 18). In *Acacia farnesiana* both the diploid and tetraploid strains (Ghimpu 1929) were studied (figs. 23 and 25). In both strains polyploid divisions were common in the root meristem early in development (figs. 23 to 26). There was no evidence of paired chromosomes in these divisions. In all the above

[2] This greenhouse was erected with funds contributed by the ESSO Foundation.

TABLE 1. *List of genera studied. The diploid chromosome number of each species as listed in the "Chromosome Atlas of Flowering Plants" by Darlington and Wylie is given. The source of the seed is also indicated in parentheses after the specific name. G.P.S.—Geo. Park Seed Company; L.H.B.P.—Lembaga Hortus Botanicus Pusat; G.G.C.—G. Ghose and Co.; N.Y.B.G.—New York Botanical Garden; G.B.S.H.—General Biological Supply House; S.I.—Smithsonian Institution, Washington, D.C.; U.S.D.A.—United States Department of Agriculture; W.A.B.C.—W. Atlee Burpee Co.*

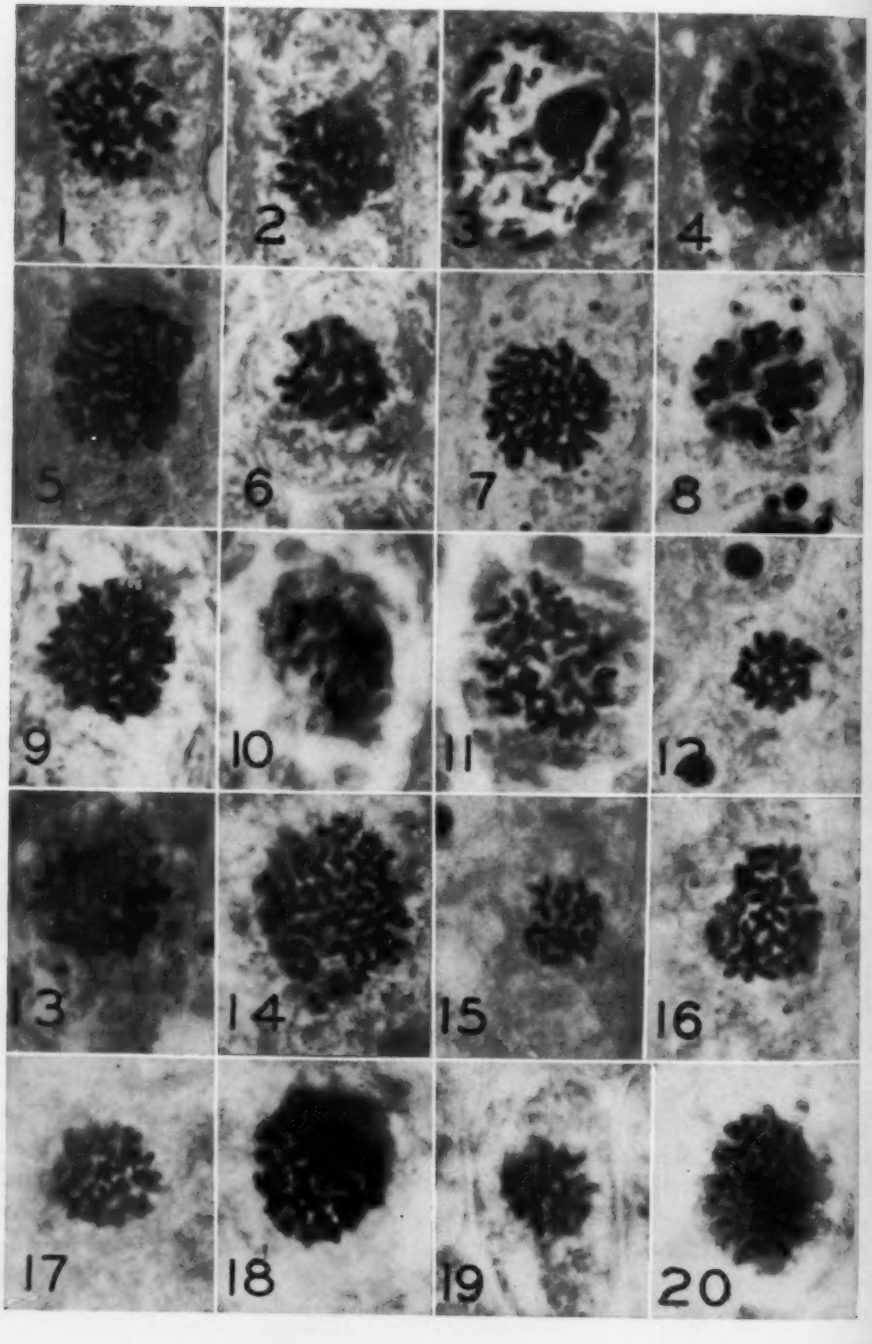
Mimosoideae	
Schrankia uncinata (G.P.S.)	
Enterolobium timbouva (L.H.B.P.)	26
Piptadenia peregrina (L.H.B.P.)	
Acacia catechu (G.G.C.)	26
farnesiana (L.H.B.P.)	52
Albizzia lophantha (N.Y.B.G.)	26
julibrissin (N.Y.B.G.)	26
Pithecolobium hystrix (L.H.B.P.)	
Leucaena tricodes (L.H.B.P.)	
Mimosa palmeri (U.S.D.A.)	
pudica (G.B.S.H.)	52
Neptunia plena (L.H.B.P.)	c72
Caesalpinioideae	
Cercis chinensis (N.Y.B.G.)	
Cassia corymbosa (N.Y.B.G.)	
marilandica (N.Y.B.G.)	
medsgeri (N.Y.B.G.)	
Sindora bruggemanniide (L.H.B.P.)	
Trachylobium verrucosum (L.H.B.P.)	16
Peltogyne paniculata (L.H.B.P.)	
Caesalpinia granadillo (L.H.B.P.)	
pulcherrima (L.H.B.P.)	24
sappan (L.H.B.P.)	24
Ceratonia siliqua (G.B.S.H.)	24
Erythrophloeum guineense (L.H.B.P.)	24
Hymenaea courbaril (S.I.)	24
Intsia bijuga (L.H.B.P.)	24
Bauhinia purpurea (G.G.C.)	28
tomentosa (G.G.C.)	
ungulata (U.S.D.A.)	
variegata (L.H.B.P.)	28
Delonyx regia (G.G.C.)	28
Dialium indica (L.H.B.P.)	
Gleditsia triacanthos (N.Y.B.G.)	28
Gymnocladus dioica (N.Y.B.G.)	28
Parkinsonia aculeata (S.I.)	28
Peltophorum inerme (L.H.B.P.)	28
Papilionoideae	
Vicia faba (W.A.B.C.)	12
Pisum sativum (W.A.B.C.)	14
Lathyrus latifolius (N.Y.B.G.)	14
maritimus (N.Y.B.G.)	14
Lespedeza hirta (N.Y.B.G.)	20
Desmodium sambuense (G.G.C.)	
Aeschynomene indica (S.I.)	40
virginica (S.I.)	40
sensitiva (S.I.)	20
elegans (S.I.)	20
brasiliana (S.I.)	20
pratensis (S.I.)	20
Trifolium album (N.Y.B.G.)	
Parochetus communis (N.Y.B.G.)	16

TABLE 1. (*con't*)

Sesbania aegyptica (G.G.C.)	12
Indigofera dosua (G.G.C.)	16
amblyantha (N.Y.B.G.)	16
Colutea melanocalyx (N.Y.B.G.)	
orientalis (N.Y.B.G.)	
persica (N.Y.B.G.)	
Wisteria floribunda (N.Y.B.G.)	16
frutescens (N.Y.B.G.)	16
sinensis (N.Y.B.G.)	16
Caragana microphylla (N.Y.B.G.)	
Robinia fertilis (N.Y.B.G.)	20
hartwigii (N.Y.B.G.)	20
Amorpha fruticosa (N.Y.B.G.)	40
Baptisia australis (N.Y.B.G.)	18
Piptanthus nepalensis (N.Y.B.G.)	18
Thermopsis caroliniana (N.Y.B.G.)	
Crotalaria alata (G.G.C.)	16
Lupinus polyphyllus (W.A.B.C.)	48
Cytisus scoparius (N.Y.B.G.)	24, 46, 48
Genista monosperma (N.Y.B.G.)	48
Sophora japonica (N.Y.B.G.)	28
viciifolia (N.Y.B.G.)	
Cladrastis lutea (N.Y.B.G.)	28
Vigna sesquipedalis (N.Y.B.G.)	24
Phaseolus lunatus (W.A.B.C.)	22
vulgaris (W.A.B.C.)	22
Pueraria javanica (G.G.C.)	22, 24
Erythrina lithosperma (G.G.C.)	
Maackia amurensis (N.Y.B.G.)	

the polyploid divisions occurred in the periblem region of the root meristem. The range of these divisions is given in table 2. In *Pithecolobium hystrix*, polyploid divisions were also present in the large central cells of the plerome. The one exception to this type of development was found to be *Piptadenia peregrina*. Although polyploid divisions were also found in the root meristem of this species they were not nearly as common as the polyploid divisions in the other species of the Mimosoideae. This, however, was also found to be true of the diploid divisions.

Subfamily Caesalpinioideae. In the subfamily Caesalpinioideae, polyploid divisions were common in the root meristem in the early germination of the seeds of *Cassia corymbosa, Cassia marilandica, Cassia medsgeri, Delonyx regia* and *Parkinsonia aculeata* (figs. 10, 11, 33 to 38). These polyploid divisions as in all the Mimosoideae were most common in seedlings 4 mm. in length. No polyploid divisions were found in the early development in *Cercis chinensis, Bauhinia purpurea, Bauhinia tomentosa, Bauhinia ungulata, Bauhinia variegata, Ceratonia siliqua, Dialium indica, Erythrophloem guineense, Sindora bruggemanniide, Trachylobium verrucosum, Peltogyne paniculata, Hymenaea courbaril, Intsia bijuga, Gymnocladus dioica, Gleditsia triacanthos, Peltophorum inerme, Caesalpinia granadillo, C. pulcherrima, C. sappan.* In *Cassia medsgeri, Cassia marilandica, Delonyx*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regia and *Parkinsonia aculeata* tetraploid divisions only were found. In *Cassia corymbosa*, on the other hand, octoploid divisions as well were found. There was some evidence of pairing in the prophases of the polyploid divisions. At metaphase the paired association was no longer evident (figs. 11, 34, 36 and 38). Figures 10, 33, 35 and 37 are diploid metaphases found in the same region of the root meristem.

Subfamily Papilionoideae. With one exception polyploid divisions in early development were not found in any of the species studied belonging to the Papilionoideae. Occasional polyploid divisions, however, were found in the region of elongation and differentiation. This was found to be true in the case of *Erythrina lithosperma* (figs. 39 and 40). A similar condition was noted previously in a number of genera in the Papilionoideae by several investigators. Iyengar (1939) noted occasional tetraploid divisions in the periblem region of the root tip of *Cicer arietinum*. Wipf and Cooper (1940) reported occasional tetraploid divisions in the root hair region of *Pisum sativum, Lathyrus latifolius, Lathyrus odoratus, Vicia villosa* and *Lespedeza tomentosa*. The cells with the tetraploid number of chromosomes were usually closely adjacent to the endodermis, but occasionally they were found in the outer layers of the parenchyma near the primordia of secondary roots. Polyploid divisions were found in early development in *Aeschynomene*. Sufficient seeds, however, could not be obtained for a more detailed study.

Discussion. The observations here reported on the time and place of polyploid divisions in the development of diploid plants may serve as a new criterion in the further classification of the Leguminosae. In a number of leguminous plants previously investigated polyploid divisions were found to be common in the root meristem of seedlings 2 to 6 mm. in length. As the seedlings increased in length these cells differentiated as polyploid cells and the later divisions in the meristem are diploid divisions.

In all the species studied belonging to the Mimosoideae polyploid divisions were common in the root meristem in early development. In the Caesalpinioideae only three genera showed a similar condition: *Cassia, Delonyx* and *Parkinsonia*. The other genera in the Caesalpinioideae did not

FIGS. 1–20. Photomicrographs of iron alum hematoxylin stained sections of divisions from the root meristem of various species of Leguminosae. Magnification × 1750. FIG. 1. *Mimosa pudica*, 2n Metaphase. FIG. 2. *Mimosa pudica*, 2n Metaphase. FIG. 3. *Mimosa pudica*, 4n Prophase. FIG. 4. *Mimosa pudica*, 4n Metaphase. FIG. 5. *Mimosa pudica*, 4n Metaphase. FIG. 6. *Albizzia julibrissin*, 2n Metaphase. FIG. 7. *Albizzia julibrissin*, 4n Metaphase. FIG. 8. *Albizzia julibrissin*, 4n Paied Metaphase. FIG. 9. *Albizzia julibrissin*, 4n Metaphase. FIG. 10. *Cassia marilandica*, 2n Metaphase. FIG. 11. *Cassia marilandica*, 4n Metaphase. FIG. 12. *Schrankia uncinata*, 2n Metaphase. FIG. 13. *Schrankia uncinata*, 4n Metaphase. FIG. 14. *Schrankia uncinata*, 8n Metaphase. FIG. 15. *Acacia catechu*, 2n Metaphase. FIG. 16. *Acacia catechu*, 4n Metaphase. FIG. 17. *Acacia catechu*, 4n paired Metaphase. FIG. 18. *Acacia catechu*, 8n paired Metaphase. FIG. 19. *Enterolobium timbouva*, 2n Metaphase. FIG. 20. *Enterolobium timbouva*, 4n Metaphase.

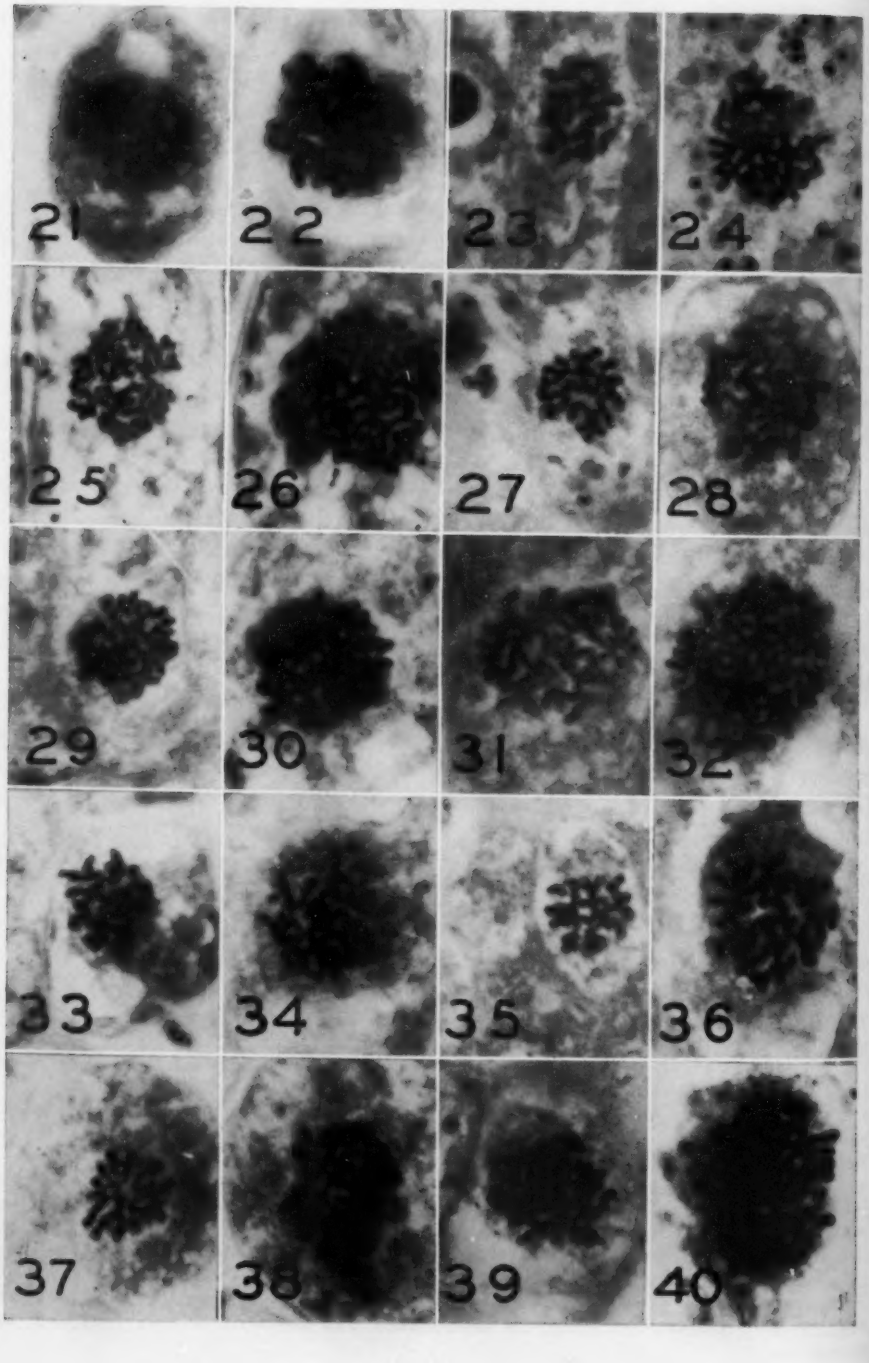
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TABLE 2. *List of genera having polyploid divisions in development. The distance in microns from the tip is given for the first and last diploid divisions, the first and last polyploid divisions.*
pr—paired; un—paired.

Genus	2n		4n		8n	
	First	Last	First	Last	First	Last
Schrankia uncinata	480	1200	680(pr)	1088(pr)	812(pr)	1168(pr)
			656(un)	1328(un)	872(un)	1112(un)
Enterolobium timbouva	512	1416	1000(pr)	1400(pr)		
			1024(un)	1408(un)		
Piptadenia peregrina	552	1416	1000(un)	1120(un)		
Acacia catechu	368	1536	576(pr)	1488(pr)	1080(pr)	1344(pr)
			696(un)	1296(un)	952(un)	1360(un)
Acacia farnesiana 2n–26	344	1200	776(un)	1200(un)	912(un)	1008(un)
Albizzia lophantha	312	1160	776(pr)	1048(pr)		
			600(un)	1160(un)		
Pithecolobium hystrix	720	1608	1144(pr)	1488(pr)		
			1232(un)	1512(un)		
Leucaena tricodes	488	1392	864(pr)	1328(pr)		
			944(un)	1376(un)		
Mimosa palmeri	344	1160	536(pr)	984(pr)	1000(pr)	1032(pr)
			488(un)	1128(un)		
Neptunia plena	248	1152	686(pr)	1096(pr)		
			702(un)	1120(un)		
Cassia corymbosa	128	760	232(pr)	744(pr)		
			264(un)	736(un)		
Cassia marilandica	248	1064	576(pr)	1000(pr)		
			648(un)	992(un)		
Cassia medsgeri	184	832	408(pr)	672(pr)		
			416(un)	784(un)		
Delonyx regia	336	1488	712(pr)	1472(pr)		
			608(un)	1456(un)		
Parkinsonia aculeata	280	1200	488(pr)	1176(pr)		
			464(un)	1136(un)		

show any polyploid divisions in the root meristem early in development. This might indicate that *Cassia*, *Delonyx* and *Parkinsonia* are more closely related to the Mimosoideae than they are to the other Caesalpinioideae. By the taxonomists *Cassia* is placed in the tribe Cassieae and both *Parkinsonia* and *Delonyx* are in the tribe Kramerieae. Other genera in both these tribes

FIGS. 21–40. Photomicrographs of iron alum hematoxylin stained sections of divisions from the root meristem of various species of Leguminosae. Magnification × 1750. FIG. 21. *Piptadenia peregrina*, 2n Metaphase. FIG. 22. *Piptadenia peregrina*, 4n Metaphase. FIG. 23. *Acacia farnesiana*, 2n Metaphase of the diploid strain. FIG. 24. *Acacia farnesiana*, 4n Metaphase of the diploid strain. FIG. 25. *Acacia farnesiana*, 2n Metaphase of the tetraploid strain. FIG. 26. *Acacia farnesiana*, 4n Metaphase of the tetraploid strain. FIG. 27. *Pithecolobium hystrix*, 2n Metaphase. FIG. 28. *Pithecolobium hystrix*, 4n Metaphase. FIG. 29. *Leucaena tricodes*, 2n Metaphase. FIG. 30. *Leucaena tricodes*, 4n Metaphase. FIG. 31. *Neptunia plena*, 2n Metaphase. FIG. 32. *Neptunia plena*, 4n Metaphase. FIG. 33. *Cassia corymbosa*, 2n Metaphase. FIG. 34. *Cassia corymbosa*, 4n Metaphase. FIG. 35. *Cassia medsgeri*, 2n Metaphase. FIG. 36. *Cassia medsgeri*, 4n Metaphase. FIG. 37. *Parkinsonia aculeata*, 2n Metaphase. FIG. 38. *Parkinsonia aculeata*, 4n Metaphase. FIG. 39. *Erythrina lithosperma*, 2n Metaphase. FIG. 40. *Erythrina lithosperma*, 4n Metaphase.

did not show polyploidy in development. In the Papilionoideae polyploid divisions were found in the early development of seedlings of *Aeschynomene*. Sufficient seeds of this genus, however, could not be obtained for a detailed study. No other genus in this subfamily showed polyploid divisions in the root meristem in early development. Wipf and Cooper (1940) found polyploid divisions in a number of genera belonging to this subfamily. These divisions were not found in the meristem, however, but in the root-hair region. In the species studied by them—*Lathyrus latifolius, Lathyrus odoratus, Lespedeza tomentosa* and *Vicia villosa* occasional tetraploid divisions were found 4.6 mm. (4600 microns) back from the growing tip. In the present study as indicated in table 2 the first tetraploid divisions occurred about 668 microns or 0.67 mm. from the tip and the last 1180 microns or 1.18 mm. This is well within the meristematic region. In the present study occasional polyploid divisions were noted in the root hair region of several of the Papilionoideae.

SUMMARY

1. Seventy-nine species from fifty-five genera representative of the three subfamilies of the family Leguminosae were studied.

2. In the subfamily Mimosoideae, in all species studied polyploid divisions occurred at the beginning of the mitotic activity in the root meristem. As the seedlings increased in length these divisions decreased in number.

3. In the subfamily Caesalpinioideae, polyploid divisions were found early in development of *Delonyx, Cassia* and *Parkinsonia*. Polyploid divisions were not found in *Cercis chinensis, Bauhinia purpurea, Bauhinia tomentosa, Bauhinia ungulata, Bauhinia variegata, Ceratonia siliqua, Dialium indica, Erythrophloem guineense, Sinodora bruggenanniide, Trachylobium verrucosum, Peltogyne paniculata, Hymenaea courbaril, Intsia bijuga, Gymnocladus dioica, Gleditsia triacanthos, Peltophorum inerme, Caesalpinia granadillo, C. pulcherrima, C. sappan.*

4. In the subfamily Papilionoideae, polyploid divisions were found in the root meristem of young seedlings of only a single genus, *Aeschynomene*. Sufficient seeds, however, could not be obtained for a detailed study.

5. It is suggested that the presence or absence of polyploid divisions in the development of diploid species may be a new and useful criterion for taxonomic studies.

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THE TRACHEARY ELEMENTS OF EQUISETUM WITH OBSERVATIONS ON THE ONTOGENY OF THE INTERNODAL XYLEM[1]

DAVID W. BIERHORST

Despite the fact that a large number of publications have appeared on the anatomy of *Equisetum* there remains much more to be done. As far as certain structural features are concerned, some of the fossil articulates are better known than are the extant *Equiseta*. A very satisfactory description of the tracheary elements of *Equisetum* in 1900 may have been that they are annular, helical, or somewhat reticulate, but the emphasis which has been placed on other characteristics of primary xylem elements since that time (Bailey 1925, 1949) necessitates a more detailed description of these elements in the genus *Equisetum*.

Nomenclatural difficulties are impossible to avoid in the present description. The two terms which stand out in this context are protoxylem and metaxylem. Extensive discussions dealing with the history of these terms as well as the various ways in which they have been applied are presented by Bugnon (1925) and Esau (1943). It seems advisable merely to state precisely how the terms are to be used here, how the definitions differ from those currently applied, and the major reasons for the discrepancies.

The question could be raised as to whether or not there is a definite need for the terms protoxylem and metaxylem; the proper answer seems to be an unqualified yes. In general, regardless of which of the various definitions are adhered to, the protoxylem is the significant water conducting tissue (exclusive of parenchyma, and undifferentiated procambium) in both the region of elongation and those tissues located more distally. On the other hand, the metaxylem becomes more significant in the more proximal regions. As a necessary consequence of this, the various selective factors operating on the protoxylem do not correspond exactly with those operating on the metaxylem, and therefore morphological divergence is to be expected. It seems logical to state that natural selection in the protoxylem favors stretchability and also the ability of an element to maintain an open lumen following some stretching. Conversely, it would seem logical to state that selection in the metaxylem favors elements with more extensive secondary walls, mechanical support of the organ becoming of significance at this level. The above assumptions would be most meaningful in an organ devoid of other mechanical tissue in the mature regions.

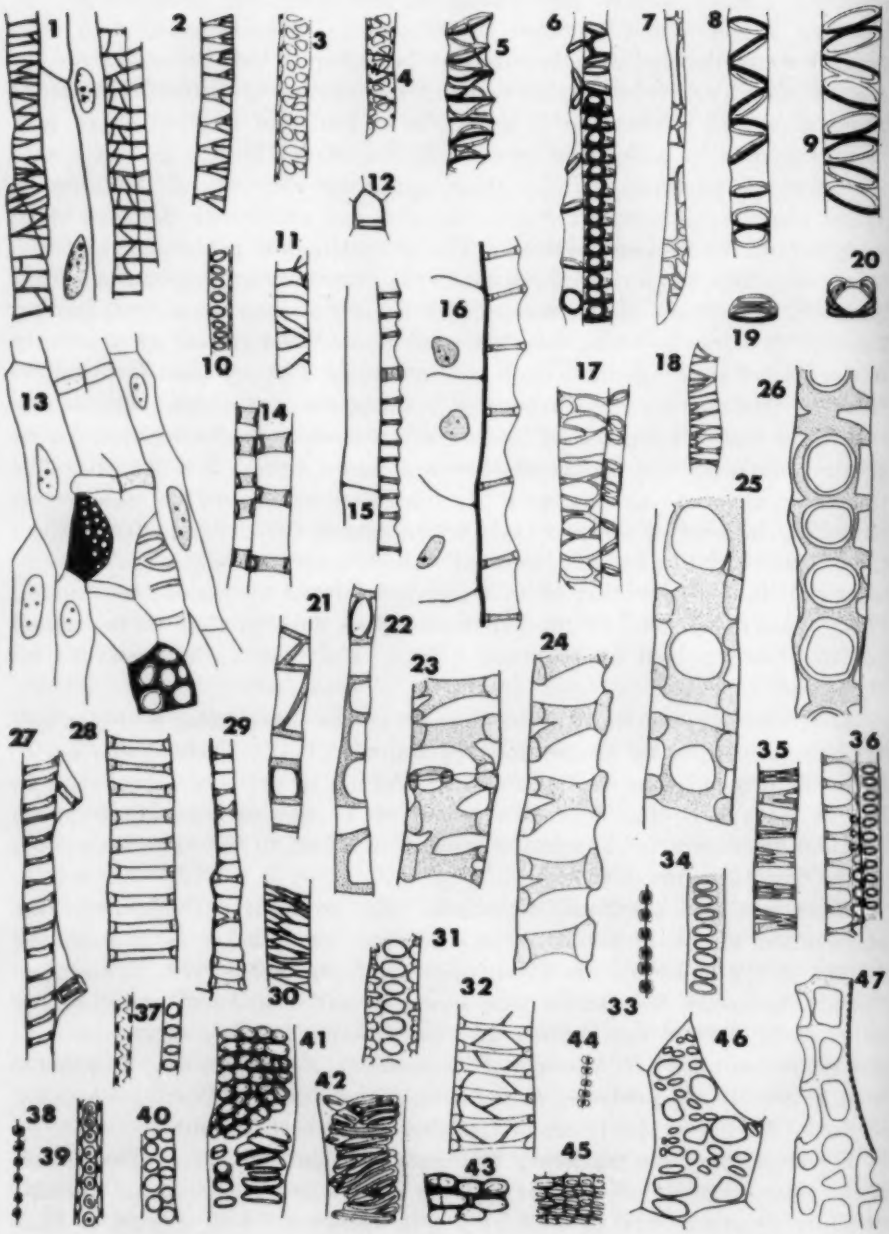
[1] This work was begun at the Samuel Miller Biological Laboratories of the University of Virginia.

Esau (1953) defines protoxylem as including the elements of the primary xylem which undergo stretching, i.e., passive elongation. She further states that helical elements may be either in the protoxylem or the metaxylem. She therefore makes no strict morphological distinction between protoxylem and metaxylem. It cannot be argued that a given organ may be inhibited in its elongation by altering the environment, e.g., water supply, chemical treatment. Under these conditions elements of the primary xylem which were completely differentiated and previously destined to be stretched do not become stretched. The morphological nature of these elements certainly has not been changed; they are still protoxylem elements. *Eichhornia crassipes* as an example is usually known as a free floating aquatic. It often, however, becomes established for a period on relatively dry soil after an appreciable drop in water level. The dry-land form differs from the free-floating form primarily in the absence of appreciable elongation in its various organs, in its much less aerenchymatous tissue, in its greater firmness, and in its thicker and more lignified cell walls. The tracheary elements are structurally identical save for the absence of stretching in some of the protoxylem elements of the dry-land form. Esau (1953) points out in her discussion of wall structure in relation to development that if the elongation of an organ is inhibited by various techniques, pitted elements instead of the extensible types develop close to the apical meristem as reported by Goodwin (1942), Koernike (1905), and Smith and Kersten (1942).

It follows that the most usable concept of the protoxylem is that which has been presented by Eames and MacDaniels (1947). They define protoxylem strictly in terms of stretchability, and not in terms of actual stretching. It is obvious that regardless of which of the various definitions is followed subjective interpretation must be applied to the transition from protoxylem to metaxylem.

Materials and methods. Details of the procedures followed in the preparation of the material for microscopic examination as well as the sources of the materials are given elsewhere (Bierhorst 1958). The material of *Equisetum laevigatum* was, however, not mentioned, and this was collected in 1949 in the Batture at New Orleans, La. The species used in this study included: *E. hyemale, E. kansanum, E. laevigatum, E. sylvaticum, E. arvense, E. pratense, E. palustre, E. variegatum, E. scirpoides,* and *E. fluviatile.* Whole specimens of the above have been retained.

Description of the tracheary elements. The carinal group. The carinal protoxylem elements of each of the ten species studied were all annular without exception (figs. 13–16.) This is in agreement with reports of Hofmeister (1862) and Vidal (1912), but Goebel (1887), Golub and Wetmore (1948), and Johnson (1933) reported the presence of helical elements in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this position. The structure of the annular thickenings did vary in structure within species as well as among the various species. The variations among the annular thickenings are best described from a sectional view of the ring itself, i.e., the view one would get by focusing on the sides of an element which was cut in the longitudinal plane.

The rings of the secondary wall varied from semicircular (figs. 15, 16) to flat and elongate (fig. 14) in sectional view, with a wide range in size in each shape category. Massive, flattened rings were most characteristic to the exclusion of other types in *E. scirpoides* and *E. variegatum*, but were also to be found in *E. hyemale*, *E. kansanum*, and *E. laevigatum*. The broad, flattened rings are rarerly uniform in thickness; this can be seen in the sectional view (fig. 14) or in the face view by observing lighter and and darker stained areas. Occasional openings occur within the broader rings (fig. 64).

As a general characteristic, the rings of the annular tracheary elements of the carinal protoxylem are thicker in the rhizome than in the aerial stem.

A feature of the primary wall of the tracheary elements is noted in the carinal protoxylem which is also true for most of the tracheary elements of all the species studied. This is the tendency for the primary wall to become conspicuously thickened in those areas where the secondary wall is in contact (fig. 65). The thickening of the primary wall can be seen before any sign of secondary wall deposition. In the carinal protoxylem elements thickened primary walls are not only noted where there is secondary wall, but also between the rings of the secondary wall on the sides of the elements which are away from the carinal canal (fig. 16).

Within a given element, the rings often vary in size. Figure 15 shows a portion of an element which has some wide rings and others narrower.

FIGS. 1–47. FIGS. 1–12. Tracheary elements of the leaves of *Equisetum*. FIGS. 1, 2. *E. sylvaticum*. FIGS. 3, 4, 10–12. *E. variegatum*. Trabeculae are shown in figures 3 and 12. FIG. 5. *E. palustre*. FIGS. 6, 8, 9. *E. kansanum*. FIG. 13. Carinal region just above the 9th node in an aerial shoot of *E. kansanum*. FIGS. 14–16. Carinal protoxylem of the internode of *Equisetum*. FIG. 14. *E. kansanum*. FIGS. 15, 16. *E. sylvaticum*. FIGS. 17, 18. Trans-nodal protoxylem of *Equisetum*. FIG. 17. *E. kansanum*. FIG. 18. *E. sylvaticum*. FIGS. 19, 20. Diagrams of secondary wall annular thickenings. Based on the trans-nodal protoxylem of *E. sylvaticum*. FIGS. 21–26. Carinal metaxylem of *Equisetum*. FIGS. 21, 22. *E. variegatum*. FIGS. 23–26. *E. sylvaticum*. FIGS. 24 and 25 are two views of the same element. FIG. 24 is the side of the element away from the carinal canal. FIG. 25 is the side of the element toward the canal. FIG. 26. The side of another element facing the carinal canal. FIGS. 27–40. Elements of the lateral xylem of the internode of *Equisetum*. FIGS. 27–32. *E. sylvaticum*. FIGS. 29–32 are from the rhizome. FIGS. 33–36. *E. kansanum*. FIG. 37. *E. scirpoides*. Two views of similar elements. FIGS. 38–40. *E. variegatum*. FIGS. 41–47. Elements of the nodal metaxylem of *Equisetum*. FIGS. 41–45. Tracheary elements from within the nodal mass. FIG. 41. *E. kansanum*. FIG. 42. *E. variegatum*. FIG. 43. *E. pratense*. FIGS. 44, 45. *E. sylvaticum*. FIG. 46. *E. sylvaticum*. Nodal element connecting to the lateral xylem of the internode. FIG. 47. *E. sylvaticum*. Element located on the outer edge of the nodal metaxylem. All ×390.

The border, i.e., the overlapping of the primary wall by the secondary wall, is absent or extremely inconspicuous in the carinal protoxylem elements, except where the secondary wall tends to become separated from the primary wall during the formation of the carinal canal (fig. 65).

Many of the elements of the carinal protoxylem possess transverse and extremely delicate end-walls. This makes it likely to confuse often a vertical series of tracheids with a single one. Hofmeister (1862) described the horizontal septa as being absorbed, resulting in a group of annular vessels. It was found in the present study that with critical staining the end walls are always identifiable. There are occasional first-formed annular elements in all of the species examined which traverse the entire length of the internode as Barratt (1920) recorded for *E. arvense*.

Adjacent to the carinal canal and located toward the outside of but slightly shifted to each side of the carinal protoxylem, are generally one to 4 tracheary elements which are referred to here as the carinal metaxylem (figs. 21–26, 63). They are characteristically present in all of the ten species studied. Their constant positions are in the upper and lower portions of the internodes, but they often differentiate throughout the internode after all intercalary growth has ceased. Their presence bears no relationship to the presence or absence of the lateral xylem of the internodal bundle. They are considerably larger than the elements of the carinal protoxylem (fig. 63). In structure they are of a highly modified annular type. The rings are massive and thick, but only slightly flattened. Between the rings, the secondary wall outlines large circular pits which may be simple or bordered, even in the same species. The pits of all of the species studied except *E. variegatum* and *E. fluviatile* are regularly situated on the carinal canal side of the elements whereas no pits were observed on other sides. The pits are in a definite row down one side of the element. The elements possess nearly transverse end-walls (fig. 23).

In *E. variegatum*, the pits are not restricted to the canal side of the elements (fig. 22). An occasional diagonally oriented interconnection between adjacent rings was also noted in this species (fig. 21).

In *E. fluviatile*, the comparable elements were almost entirely helical with massive secondary wall thickenings. Circular pits between adjacent gyres were rare.

The elements referred to here as carinal metaxylem were mentioned by Browne (1920) and Gwynne-Vaughan (1901) as occurring in *E. giganteum*, by Duval-Jouve (1864) in *E. hyemale*, by Queva (1907) in *E. maximum*, and by Goebel (1887) in unspecified species. They were described as coarsely reticulate or broadly reticulate by Duval-Jouve (1864), Goebel (1887), and Gwynne-Vaughan (1901), as irregularly open reticulate by Barratt (1920), and annular reticulate by De Bary (1884). Duval-Jouve

(1864) illustrated these elements and indicated the large pits as not being restricted to one side of the element, but distributed at ramdom on all sides.

The carinal metaxylem elements were considered by Milde (1867), Browne (1920), Queva (1907), and Barratt (1920) as belonging to the lateral xylem of the internodal bundle. This is firmly denied here. The presence or absence of these elements bears no relation to the presence or absence of the lateral xylem nor to the proximity of the lateral xylem to the carinal xylem. It is probable that the reports of exarchy in the lateral xylem of the internodal bundle of *E. giganteum* and other species (Browne 1922), Gwynne-Vaughan (1901) and Poirault (1893) and of irregular development in *E. maximum* and other species by Queva (1907) and Eames (1909) are the results of considering the carinal metaxylem as belonging to the lateral xylem.

Elements of the leaf trace. The xylem of the leaf trace of the ten species examined was formed from a branch of the carinal xylem of the internode below, as reported by Gwynne-Vaughan (1901), Browne (1922), and Golub and Wetmore (1948). Never was it observed that either lateral xylem of the internode or nodal metaxylem contributed to the leaf trace, despite the fact that Eames (1909) and Browne (1939) reported such a contribution. Occasionally a tracheid from the nodal metaxylem will end near the point of departure of the leaf trace and bend slightly outward; this is the only indication that there may be such a contribution.

The leaf traces of the various species are usually composed of tracheary elements with variously disposed secondary walls. The simple, unmodified annular element characteristic of the carinal protoxylem of the internode of the stem is in the minority. The larger elements referred to above as carinal metaxylem are absent, but smaller elements of a somewhat similar nature are often present.

Helical elements are occasionally present in the leaf traces, but are quite uncommon, and rarely is such an element helical throughout its length. Helical elements when found are usually located near the base of the leaf or in the leaf trace before it enters the appendage. Elements which are at least in part helical are to be found in the leaf traces of *E. variegatum*, *E. scirpoides*, and *E. palustre*. The helices are simple, never double, and in a given element do not change their direction of coiling, as occurs in *Selaginella* (Zamora 1957). In these elements, where the helix is interrupted, the secondary wall is in the form of simple rather thin rings. These are the first formed elements of the leaf traces.

A wide variety of modifications of the annular element occurs in the leaf traces of *Equisetum*, some of which are superficially so similar to helical elements that they can only be distinguished from the latter by a very careful examination using the oil immersion objective.

The simplest modifications of the annular element found in the leaf trace are those derived by the union of adjacent rings in various ways within the same element. Adjacent rings may be joined at essentially one point along the circumference so that on stretching the two rings separate as if they were hinged on one side (fig. 6). Successive rings may be joined on alternating sides so that on stretching the group of rings unfolds (fig. 8). Even more striking and difficult to detect is the modification where the rings are joined to each other successively such that the points of union fall along a helix (fig. 9). Before this type of element is stretched, the points of union are often not observed, and the element is taken for a typical annular element, but after stretching it appears as a helical element. Annular elements with attached rings were found most commonly in *E. kansanum*, and in fact extensive longitudinal series of attached rings were observed only in this species. Other species possessed occasional joined rings, but usually only in pairs.

Other modifications of the annular type of tracheary element in the leaf trace are concerned with structural modifications of the individual rings, forming limited reticula. A simple example of this type of modification is shown in figure 2, where each ring has a limited reticulum on one side. Note that the branching was all on one side of the element, which was in this instance toward the adaxial side of the leaf. The element was adjoined on both sides by parenchyma. A reconstruction of a single ring of this type is shown in figure 19, which was based on the transnodal protoxylem of *E. kansanum*. Reticulate rings are present to a more or less extent in the leaf traces of all of the species examined. The more extreme examples were illustrated.

Annular elements modified from their simple condition by the presence of pits between the individual rings are very common in the leaf traces of *Equisetum*. These elements are similar to the carinal metaxylem elements, but smaller and with more uniformly disposed pits. They were observed in the leaf traces of *E. kansanum*, *E. hyemale*, *E. laevigatum*, *E. variegatum*, and *E. scirpoides*, with the most conspicuous development in the latter two species. The pits occur in very uniform vertical rows and may be simple (fig. 6) or bordered (fig. 10). The rows of pits are on the sides of the elements which border onto other tracheary elements. The number of rows varies from one to four, depending in some cases on the number of tracheary elements adjoining.

Elements which might be referred to as reticulated annular were observed in the leaf trace of *E. sylvaticum*. These are elements which possess a rather simple series of rings, but between the rings are connections of a lesser magnitude which are oriented diagonally to nearly vertically (fig. 1). It is of particular interest to note that during the development of these

elements, the series of transversely oriented rings is completely developed and lignified before the interconnections are formed.

In addition to the elements described above, there are elements in the leaf traces which are quite reticulate and whose structural characteristics give no suggestion of either annular or helical plan of organization. These range from loosely reticulate protoxylem elements (figs. 5, 7, 11), which undergo stretching, to densely reticulate metaxylem elements (figs. 3, 4). The loosely reticulate ones are most conspicuous in *E. variegatum*, *E. scirpoides*, and *E. palustre*. The secondary wall thickenings in certain of the loosely reticulate elements were so delicate that they could not be detected in a transverse section of the leaf. Stretched reticulate elements give the appearance in longitudinal section of an entangled mass of fine wire and may easily be mistaken for stretched elements with multiple helices.

The more densely reticulate elements (figs. 3, 4) give the appearance of having many pits distributed in an irregular to alternate fashion with irregularly shaped apertures.

Of particular interest is the occasional occurrence of trabeculae in the more densely reticulate elements of *E. variegatum* (figs. 4, 12). These appear as fine strands of wall material traversing the cell lumen toward one side of the cell.

Detailed descriptions of the tracheary elements of the leaf trace of *Equisetum* are entirely wanting in earlier literature. Golub and Wetmore (1948) mention the presence of spiral and annular tracheids in *E. arvense*. Howmeister (1862) states that the first elements of the leaf trace are spiral.

Elements of the trans-nodal protoxylem. These are the connections between the carinal xylem of one internode with that of the adjacent internode. These strands are a constant feature of all of the nine species of *Equisetum* whose nodes were studied (listed below). They have been recorded as being present in *E. palustre* (Vidal 1912, Browne 1922), in *E. telmateia* and *E. giganteum* (Gwynne-Vaughan 1901, Browne 1922), in *E. arvense* (Golub and Wetmore 1948), and in *E. sylvaticum* (Browne 1922); and absent in *E. kansanum* (Browne 1939), in *E. hyemale* (Browne 1922), and in *E. arvense* (Barratt 1920). Barratt (1920) states emphatically, "the protoxylem certainly does not traverse the node." Browne (1922) considers the presence of trans-nodal protoxylem to be a primitive feature within the genus. The present author considers the presence of the trans-nodal protoxylem to be a constant feature of *E. hyemale*, *E. kansanum*, *E. laevigatum*, *E. arvense*, *E. pratense*, *E. palustre*, *E. sylvaticum*, *E. scirpoides*, and *E. variegatum* and probably the remainder of the species of *Equisetum* as well. Often the detection of the trans-nodal protoxylem is rather difficult, requiring relatively young nodes.

In general the trans-nodal protoxylem is composed of elements which are structurally similar to the protoxylem elements of the leaf trace of that particular species with the qualification that the trans-nodal protoxylem elements are in general somewhat more reticulate than those of the leaf trace.

Elements which have annular thickenings are common. There are generally, however, occasional points of union between adjacent rings (fig. 17). The attached rings may be in contact with each other or the attachment may be accomplished by the addition of an extra strand of wall material oriented either vertically or diagonally (fig. 17).

Helical thickenings are very rare in the trans-nodal protoxylem. Occasionally a relatively small portion of an element will possess a limited helical thickening, the remainder of the cell having annular thickenings.

Elements in which the rings form limited reticula are common (fig. 18) in those species which possess similar features in their leaf traces. Often here, however, the individual annular reticulum is more highly branched (figs. 19, 20).

Loosely reticulate elements which suggest neither helical nor annular elements and which become stretched to leave an unanalyzable mass of strands occur in the trans-nodal protoxylem (fig. 17) as they do in the leaf trace.

Vidal (1912) describes the carinal tracheary elements of *E. palustre* as becoming reticulate in the region of anastomoses, i.e., at the nodes, with all transitions seen from annular to reticulate. Golub and Wetmore (1948) report the presence of spiral and spiral reticulate elements in the trans-nodal protoxylem of *E. arvense*.

Elements of the lateral groups of xylem of the internodal bundles. The structural variations found among the tracheary elements of the lateral xylem of the internodal bundles is as great or greater than those found among the elements of the leaf traces. The lateral xylem of the internodal bundles may be composed entirely of protoxylem, entirely of metaxylem, or a mixture of the two depending on the species as well as the position of the stem in the entire plant body. It is unfortunate that throughout the literature the lateral xylem has been referred to as "the metaxylem of the bundle" regardless of species. Some of the tracheary elements of the lateral xylem of the subterranean stem have been described as vessel members (Bierhorst 1958).

Of all of the species studied *E. fluviatile* exhibited by far the simplest structure in the lateral xylem. The elements here are mostly of the simplest annular type with a rare branching of a ring. There are in addition a few of the simplest helical types. Only protoxylem is represented. Occasional stretching results in a lateral lacuna. In the subterranean stem the lateral xylem is usually absent in *E. fluviatile*.

In *E. arvense, E. pratense,* and *E. palustre* the lateral xylem of the internodal bundles is composed of elements which are mostly annular in part and helical in part. In each of these species there is a tendency to develop interconnections between rings and gyres leading to a somewhat reticulate element. Among these three species *E. arvense* shows this tendency to the greatest degree. The thickenings in these species are rather thick, but not flat, and the thickenings are considerably thicker in the aerial stems than in the rhizomes.

In *E. kansanum, E. hyemale,* and *E. laevigatum* the lateral xylem of the internodal bundles is composed almost entirely of metaxylem elements. Helical or annular elements with rows of distinctly bordered pits predominate (figs. 34, 36), often to the exclusion of other types. The basic plan of the elements seems to be mostly annular in *E. kansanum* and helical in *E. hyemale* and *E. laevigatum*. The thickening of the primary wall often reaches an extreme in this group of species, with the secondary wall in sectional view often appearing to wrap around the thickened portion of the primary wall (fig. 33). The pits, as in the leaf traces, develop on those sides of the elements which are in contact with other tracheary elements (fig. 36).

Near the extremities of the internodes in the lateral xylem of *E. kansanum, E. hyemale,* and *E. laevigatum,* one finds the reticulate annular type of element where the rings are discrete, but each one forms a limited reticulum (fig. 35). A similar type of element was described above as occurring in the leaf traces and also in the trans-nodal protoxylem.

E. scirpoides and *E. variegatum* possess elements similar to *E. hyemale, E. kansanum,* and *E. laevigatum* in the lateral xylem, i.e., annular or helical plan elements with rows of distinctly bordered pits (figs. 37, 39, 40). They differ from the latter three species, however, in that the thickenings tend to be broad and flat. The elements also tend to be smaller in diameter and, especially in *E. variegatum,* tend to be in a rather uniform radial row. The latter feature is occasionally evident in the smaller aerial stems of *E. hyemale*. The thickenings of the primary wall are also pronounced (fig. 38), but are of a uniform semicircular shape in sectional view.

E. sylvaticum possesses a variety of elements in the lateral xylem of the internodal bundle. Simple annular elements are common (figs. 27, 28) and these are often associated with the formation of a pronounced lacuna, nearly as conspicuous as the carinal canal. Often the individual annular elements exhibit extreme variation in the thickness of the annular thickenings (fig. 29). Branching of the rings is occasional (figs. 27, 29). Annular elements with fine vertically to obliquely oriented interconnections (fig. 32) occur here as in the leaf trace as well as annular elements with vertical rows of circular pits (fig. 31). Finely reticulate elements (fig. 30) which could

not be detected in transverse section were observed as occurring both toward the inside and also toward the outside of the other elements.

Previous descriptions of tracheary elements of the lateral xylem of the internodal bundles are not few in number, but are meager in structural detail. De Bary (1884) refers to the lateral xylem as composed of annular and reticulate tracheids; Eames (1909), on *E. maximum*, as scalariform or reticulate pitted with occasional annular or spiral thickening; Barratt (1920), on *E. arvense*, *E. giganteum*, and *E. maximum*, as spiral, annular, or spiral reticulate; Queva (1907), on *E. maximum* and *E. fluviatile* (*E. limnosum*) as spiral; Johnson (1933), on *E. scirpoides*, as scalariform or having multiseriate pits; Gwynne-Vaughan (1901), on *E. giganteum*, as fine reticulate with some resembling spiral; and finally Vidal (1912), on *E. palustre*, as ranging from annular to reticulate.

Nodal xylem. There are essentially two structural types of metaxylem elements which occur within the nodal complex of each of the species of *Equisetum* studied. The first is a reticulate to pitted type with a much open reticulum or very large pits in the secondary wall (figs. 13, 46, 47). It ranges from isodiametric to slightly elongate. It occurs toward the upper and lower extremities of the node as well as around the outer surface of the nodal metaxylem. The more isodiametric cells in this category occur at the junction of the nodal metaxylem and the carinal canal, and may have disrupted pit closing membranes, i.e., may be vessel members (Bierhorst 1958). There is usually a transition of elements leading to the more open reticulate near the junction of the nodal metaxylem and the lateral xylem of the internodal bundles. The large pits or openings in the reticulum may be bordered or simple.

In those species where the leaf trace appears to go through the nodal metaxylem rather than below it, e.g., *E. sylvaticum*, the tracheary elements of the node below the leaf trace are entirely of the coarse, open reticulate type.

In *E. kansanum*, *E. hyemale*, and *E. laevigatum* certain of the near isodiametric tracheary elements of the node in contact with the carinal canals often possess, in place of the massive openings in the secondary wall, many small circular bordered pits (fig. 13).

The elements which are located more internally in the nodal complex of *Equisetum* are those which are usually referred to as nodal tracheids. They range from slightly elongate, 4 to 8 times as long as broad in *E. kansanum*, *E. hyemale*, *E. laevigatum*, *E. sylvaticum*, *E. arvense*, *E. pratense*, and *E. palustre*, to fusiform, nearly 20 times as long as broad in *E. variegatum* and *E. scirpoides*.

Surface views of these elements show what appears to be a series of distinctly bordered pits which are usually circular to slightly elongate

transversely in *E. kansanum* (fig. 41), *E. hyemale, E. laevigatum, E. sylvaticum* (fig. 45), *E. arvense, E. pratense* (fig. 43) and *E. palustre,* and elongate and transversely to obliquely oriented in *E. variegatum* (fig. 42) and *E. scirpoides.* One can find, however, some elongate pits in the nodal tracheids of all of the above species on careful examination.

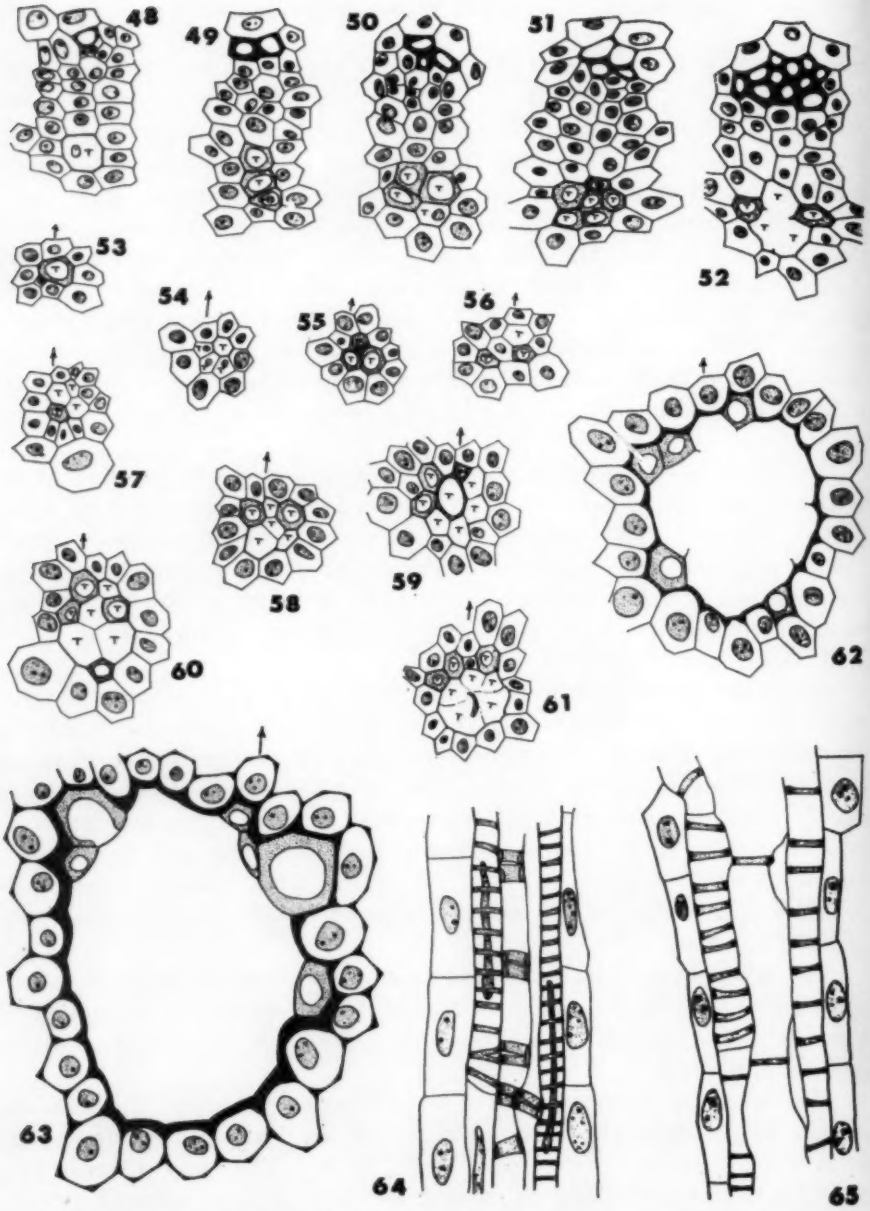
When a combination of haematoxylin, safranin, and fast green is used, the wall areas between the pits, as seen in face view, stain black or a very dark green while the pit borders stain a clear red. In a sectional view of the pits (fig. 44), it can be seen that the black areas represent the thickened primary wall which is often so pronounced in the tracheary elements located elsewhere in the body of *Equisetum.* In the younger nodes the primary wall can be seen as a thickened reticulum before secondary wall formation begins.

The short, open reticulate elements associated with the junction of the node and the carinal canal in *E. maximum* have been described by Sykes (1906). Barratt (1920) regards them as ordinary nodal tracheids. Queva (1907) mentions the occurrence of the transitional elements between the lateral xylem of the internode and the nodal metaxylem. The more typical nodal tracheids have been referred to as reticulate (Browne 1939, Queva 1907, Golub and Wetmore 1948).

Ontogeny of the internodal xylem. It is not at all possible to establish the course of differentiation of the xylem of the internodal bundle in *Equisetum* by a study of mature internodes. Transverse and longitudinal sections of mature organs of other vascular plants often clearly reveal an exarch, endarch, or mesarch pattern through which the primary xylem developed earlier. In *Equisetum,* however, the destruction and displacement associated with the development of the carinal canal removes most of the evidence upon which we can base a conclusion relative to the precise order of differentiation.

The description which follows is based on a study of serial transverse and longitudinal sections of shoot tips of *E. sylvaticum, E. kansanum, E. hyemale, E. variegatum, E. scirpoides, E. palustre, E. arvense, E. pratense,* and *E. laevigatum.*

Following the differentiation of the first annular carinal tracheid, subsequent tracheids differentiate resulting in a small group lined up radially or in a small circular group (figs. 48–52, 53–61). The exact distance from the apex in terms of internode number at which the first tracheid differentiates varies according to the activity of the apex, but it is usually in the third or the fourth internode (figs. 48, 53–55). An examination of the internodal bundles showing several tracheids partly or completely differentiated, will reveal incompletely differentiated tracheids either toward the outside or toward the inside of the first completely differentiated one. Longi-



FIGS. 48–65. FIGS. 48–52. Portions of cross-sections of vascular bundles of *E. kansanum*. A letter T is included in each of the tracheary elements. FIG. 48. 3rd internode. FIG. 49. 4th internode. FIG. 50. 4th internode. FIG. 51. 5th internode. FIG. 52. 6th internode. FIGS. 53–63. The carinal region of vascular bundles of *E. sylvaticum*. Taken from an aerial shoot not yet emerged from below the soil. FIG. 53. 4th internode. FIG. 54. 3rd internode. FIG. 55. 3rd internode. FIG. 56. 4th internode. FIG. 57. 5th internode. FIG. 58. 5th internode. FIG. 59. 6th internode. FIG. 60. 7th internode. FIG. 61. 7th internode. FIG. 62. 17th internode. FIG. 63. 20th internode. FIG. 64. Radial longitudinal section through the carinal protoxylem of *E. kansanum*, 8th internode. The pith would be located toward right. FIG. 65. Radial longitudinal section of the carinal protoxylem of *E. sylvaticum*, near the top of the 12th internode. The two tracheids on the lower left do not end at the apparent partition wall shown in the drawing, but overlap each other to a considerable extent.—All × 390.

tudinal sections will show that the first tracheids to differentiate usually extend from node to node, i.e., run the entire length of the internode, and are considerably more stretched than subsequently differentiated ones. In the drawings (figs. 48–61) the letter T is used to indicate a tracheid since they are all not obvious. Immature tracheids are shown with a nucleus. Others appear thin-walled merely because the section passed between adjacent rings of the secondary wall. In the transverse sections, it can be seen that certain tracheids expand laterally and assume a larger diameter (figs. 58, 60). This is followed by some disruption (figs. 52, 61). From the longitudinal sections, it is clear that those tracheids which are enlarging are the first which mature (fig. 65). Lacuna or carinal canal formation continues with further enlargement and disruption of the first formed tracheids (figs. 52, 61–63). It appears that the carinal canal develops as the result of first the enlargement of certain tracheids of the carinal group, then some cell separation (fig. 65) closely associated in time with the disruption of the first formed tracheids of the carinal group. This is followed by an appreciable amount of schizogenous activity and later the thickening of the walls of the parenchyma adjoining the canal.

As internode elongation precedes, some of the tracheids which matured later than early ones associated with carinal canal formation are also disrupted.

It can be stated in summary that the carinal is clearly mesarch in development as suggested for *E. hyemale* and *E. maximum* by Gwynne-Vaughan (1901) (determined here for *E. sylvaticum, E. kansanum, E. hyemale, E. variegatum, E. scirpoides, E. palustre, E. pratense,* and *E. arvense*) and not endarch as reported by Barratt (1920), Eames (1909), Queva (1907), and Golub and Wetmore (1948). Similarly, it can be stated that the carinal canal develops schizogenously and lysigenously at the onset and later primarily schizogenously, and that only a relatively few of the tracheids of the carinal protoxylem actually take part in the initial formation of the carinal canal.

In the mature internode, the tracheids which are often seen adhering to the wall of the carinal canal are those which matured latest and were not at all concerned with the formation of the canal.

Often in a cross-section, especially of *E. arvense, E. pratense, E. palustre,* and *E. sylvaticum,* of an internode where carinal canal formation has just begun, the walls of the canal-forming tracheids are so delicate as not to be observed without very critical staining. Under these circumstances, one will see what appears to be merely a ring of tracheids with the young canal on the inside. With only these observations, it is easy to erroneously conclude that the carinal canal is formed entirely schizogenously as did De Bary (1884).

The development of the lateral xylem was similarly studied for order of differentiation. In all cases this xylem developed centrifugally, with the possible exception of *E. sylvaticum* where finely reticulate elements were observed (fig. 30) in the longitudinal sections which could not be detected in the transverse sections toward the inside and also toward the outside of the other elements.

It is of particular importance to note that the large elements located adjacent to the carinal protoxylem (referred to above as carinal metaxylem) develop later in time than a portion of the lateral xylem. In other words, the centrifugal xylem of the bundle, taken in its entirety, does not mature strictly from the inside outward, but there are three distinct centers of origin, the outer two being chronologically independent of the inner one.

Discussion. It can be concluded from the foregoing descriptions that there is a broad range in variation among the tracheary elements of *Equisetum*, many of which represent rather extreme specializations. In view of these specializations, it is difficult to assume any close relationships between the living *Equiseta* and other groups of extant vascular plants. It has been suggested that there is a real affinity between *Equisetum* and *Ephedra* (Greguss 1955) based on resemblances in gross vegetative habit. It might be pointed out here that both possess helical elements with bordered pits, and this naked statement might seem to support a presumed relationship. However, the elements of *Ephedra* which have been described by Bailey (1925) as helical with bordered pits show little resemblance to the helical pitted elements of *Equisetum* save for that which is inferred in the similar terminology of the descriptions. Similarly it could be pointed out that both possess trabeculae, but this in addition does not seem sufficient to justify concluding affinity in view of the great differences between the two genera.

A comparison of the various species of *Equisetum* as to their tracheary elements reveals a close relationship among *E. hyemale*, *E. kansanum*, and *E. laevigatum*, among *E. palustre*, *E. arvense*, and *E. pratense*, and between *E. variegatum* and *E. scirpoides*. Similarly, a relationship not as close as those mentioned above between the group composed of *E. hyemale*, *E. kansanum*, and *E. laevigatum* and the group of *E. variegatum* and *E. scirpoides* is strongly suggested. These suggested relationships are mostly in accordance with systems of classification of the species (Milde 1867, Rothmaler 1944). The tendency to place *E. variegatum* and *E. scirpoides* in different sections, however, does not seem to be supported by a study of their tracheary elements.

Equisetum sylvaticum in many respects is the most specialized in its tracheary structure of the various species studied. It is interesting to note here that *E. sylvaticum* is the only species studied in which the main axis

of the vegetative shoot is completely preformed while still below the soil; the apex of the main stem is often completely aborted before the shoot emerges. This extreme specialization of complete preformation is closely approached by *E. arvense*, *E. palustre*, and *E. pratense*, where all but a relatively few nodes and internodes are established in the subterranean bud before the aerial shoot emerges. In the *hyemale* group of species, approximately ½ to ⅔ of the nodes and internodes in a particular shoot are preformed in the subterranean bud.

One commonly thinks of a series of tracheary elements within the primary xylem beginning with annular elements and going through circular-bordered pitted elements. The complete series is regarded as annular, helical, reticulate, scalariform-reticulate, scalariform-bordered pitted, and circular-bordered pitted. It is well known that the series varies in completeness in various vascular plants (Bailey 1925, 1949). The series is described in terms of increasing amount of secondary wall material. This is an accurate way of describing the transition. However, there is the inference that a given element in the series is essentially the same as the preceding one with a little more secondary wall. This may or may not be the case, even where the series is amazingly complete. There is also an occasional phylogenetic inference allied to the transition. This is especially true when a statement to the effect that certain Psilophytes as *Asteroxylon* possess only helical elements in their primary xylem is included in the description.

Often in flowering plants one finds a series of primary xylem elements from helical to circular-bordered pitted including essentially helical elements with a few interconnections between gyres, helical elements with increasing numbers of interconnections leading to a reticulum in the secondary wall, this in turn leading to more elaborate types of elements. Here it seems logical to conclude that the more elaborate types of elements are likely phylogenetic modifications of the simple helical elements.

The suggestion that there are three basic types of primary xylem elements among vascular plants, the *primitive annular element*, the *primitive helical element*, and the *primitive reticulate element*, and that these are phylogenetically unrelated seems plausible. The primitive reticulate element is not to be confused with the various derived reticulate elements which may be derived either from annular or helical elements. If it is assumed that there are three basic types of patterns of wall sculpture, it follows that there are three basic kinds of physiological patterns existing in procambial cells preceding wall differentiation. In *Equisetum* the pattern is often established in the primary wall thickenings before secondary wall formation commences. It also follows that patterns may become somewhat intermingled in the same cell, e.g., those which develop annular as well as

helical thickenings. The concept of three basic types of patterns of wall thickening in tracheary elements is based primarily on the observation of the three specialization series present in the genus *Equisetum*, one from annular through pitted, a second from helical through pitted, and a third from finely reticulate through closely reticulate or pitted, and also lack of evidence for any real relationships among the three.

The ordinary nodal tracheary elements of *Equisetum* clearly fall in the reticulate series of specialization. It is quite possible that the isodiametric to slightly elongate, coarsely or open reticulate elements which occur above and below the nodes as well as toward the outsides of the nodes, and which are occasionally living at maturity, are specialized non-tracheary elements.

SUMMARY

1. The tracheary elements of ten species of *Equisetum* are described, in addition to the development of the internodal xylem of the stem in nine species.

2. The tracheary elements are quite diverse and many are highly specialized. They range from simple annular through pitted, simple helical through pitted, and finely reticulate through pitted. They are considered as three separate series of specialization, phylogenetically unrelated. Many of the simple annular elements are modified by the union of adjacent rings in various ways as well as by the dissection of the individual rings.

3. The carinal xylem is mesarch in development while the lateral xylem of the internodal bundle is endarch. The lateral xylem is chronologically independent of the carinal xylem. The carinal xylem as well as the lateral xylem may be composed of both protoxylem and metaxylem.

4. The results indicate that among those species studied the groups composed of *E. hyemale, E. kansanum,* and *E. laevigatum; E. arvense, E. pratense,* and *E. palustre;* and *E. variegatum* and *E. scirpoides* are intrarelated closely. In addition, it is indicated that the *hyemale* group is relatively close to *E. variegatum* and *E. scirpoides.*

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HISTOGENETIC EFFECTS OF 2,3,5 TRIIODOBENZOIC ACID ON THE SHOOT APICES AND LEAF PRIMORDIA OF TOMATO[1, 2]

PAUL P. BEDESEM, JR.

The present knowledge of normal shoot apical structure and differentiation in vascular plants is extensive, particularly in the angiosperms. During the past two decades, many descriptive studies of shoot apical meristems have been reported in the literature (Philipson 1949 and Gifford 1954). Careful studies of abnormal apical structures and their development are now needed to cast light on the extent to which normal tissues may be modified without bringing about the death of the plant. A number of abnormal structures occurring naturally or induced experimentally have already been observed and described. Wardlaw (1952, 1957a, and 1957b) reviewed and summarized many of these reports.

The native auxin, indoleacetic acid, has been found, in many cases, to have a pronounced morphological effect when added to the amount already present in the plant. A number of synthetic organic chemicals are also known to induce morphogenetic responses. The best known of these form-modifying compounds are the B-naphthoxy, phenoxy, and benzoic acid derivatives, especially B-naphthoxyacetic acid, 2,4 dichlorophenoxyacetic acid, and 2,3,5 triiodobenzoic acid. Many reports in the literature describe external form changes and, in some cases, histological changes induced by indoleacetic acid and synthetic growth substances (Thomson 1945, Audus 1953, and Linser, Frohner and Kirschner 1953). Of these, 2,3,5 triiodobenzoic acid has been of particular interest since it was reported to induce or promote flowering in tomato (Zimmerman and Hitchcock 1942, 1949 a; deWaard and Roodenburg 1948) and to induce ring fasciations in the same species (Gorter 1951).

Despite the many publications in this field, there still seems to be a need for additional studies in which the development of abnormalities is observed in great detail microscopically. This is particularly true of morphological features which appear to have resulted from the differential development of two or more tissues rather than simply from an overall increase or reduction in the size of plant organs.

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The author wishes to express his gratitude to Professor E. B. Matzke for his advice and encouragement during the course of this study.

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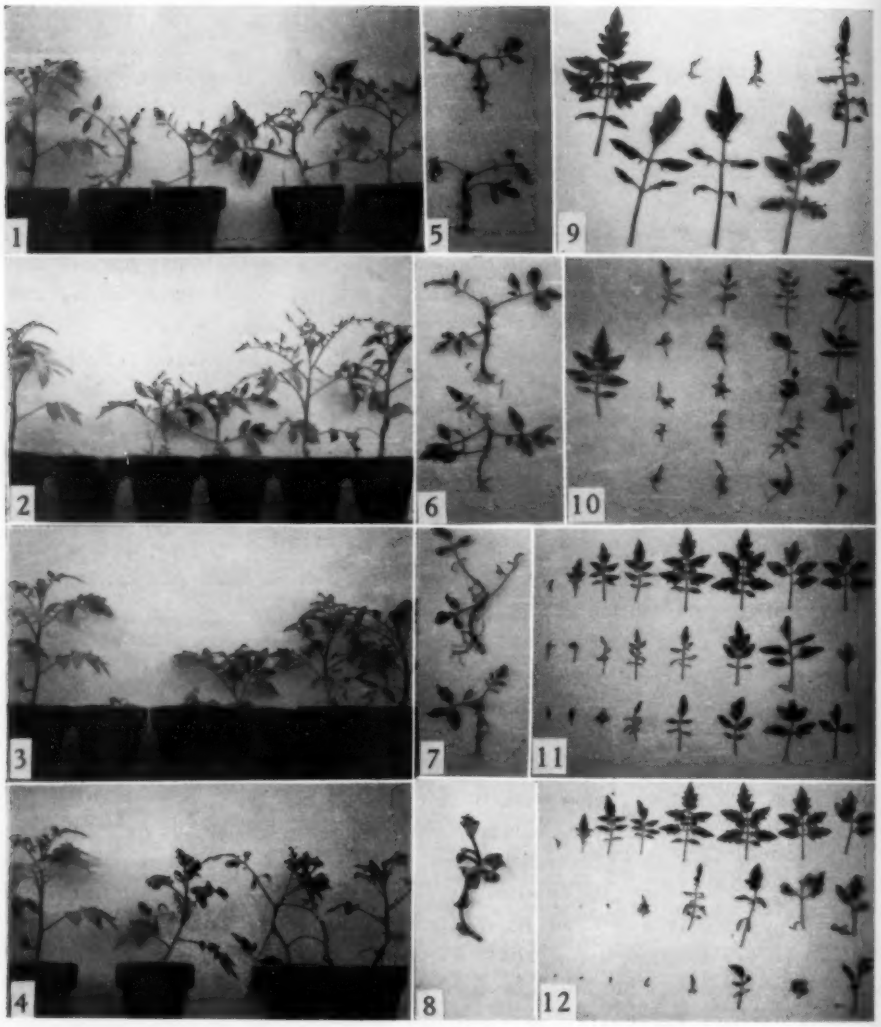
Materials and methods. In the preliminary investigations, *Bellis perennis, Coleus Blumei,* lentil, mungo bean, nasturtium, garden pea, snapdragon, soybean, squash, stock, sunflower, and tomato were treated with a number of synthetic growth substances, and the morphological alterations examined and compared. The growth modifying compounds used were α-naphthalene acetic acid; B-naphthoxyacetic acid; 2,4 dichlorophenoxyacetic acid; maleic hydrazide; N-1 naphthyl phthalamic acid; para-chlorobenzoic acid; 2,5 dichlorobenzoic acid; 2,3,6 trichlorobenzoic acid; and 2,3,5 triiodobenzoic acid.[3] These were applied in lanolin or as soil solutions over wide ranges of concentration. Reports in the literature reveal that, although many plants are affected in gross form to some degree by many of the above compounds, only a few plants are altered conspicuously or radically. This was confirmed here, since, under the conditions of these treatments, tomato was the only plant to be strikingly affected.

It was then decided to concentrate on tomato as the plant material of greatest use in this study. The chemicals to be used for further testing were narrowed down to B-naphthoxyacetic acid, 2,4 dichlorophenoxyacetic acid, N-1 naphthyl phthalamic acid, and 2,3,5 triiodobenzoic acid on the basis of the greatest and most consistent morphogenetic responses observed in the treated plants, particularly in tomato. A further preliminary investigation was then carried on to determine the relative effects of these chemicals under more carefully controlled conditions of application. The four growth-modifying substances were suspended in liquid lanolin which was then placed in a freezing compartment to harden and was subsequently cut into blocks of uniform size. These blocks were attached to the cotyledonary nodes of the tomato plants chosen for treatment. All of these compounds seemed to produce similar though not identical morphological modifications of developing leaves at their most effective, non-lethal concentrations. The most severely affected leaves showed considerable reduction in the amount of expansion and lobing of the leaflet blades, a relative increase in the amount of veining, partial or complete inhibition of lateral leaflets, and general dwarfing of the youngest leaves (figs. 1–12). Of the four chemicals used, 2,3,5 triiodobenzoic acid (TIBA) was the one which seemed to alter the shoot apical configuration most significantly.

The decision was then made to use TIBA and 2,4 dichlorophenoxyacetic acid (2,4-D) as the chemical materials for treatment in the main part of this study. Further interesting results with TIBA were indicated by the author's preliminary observations and the reports of Gorter (1949 and

[3] Drs. P. W. Zimmerman and A. E. Hitchcock of the Boyce Thompson Institute for Plant Research generously provided the author with the compounds used in these earlier studies.

The Naugatuck Chemical Division of the United States Rubber Company donated additional amounts of N-1 naphthyl phthalamic acid.



FIGS. 1–12. Photographs of tomato plants and plant parts after treatment with various growth substances. FIG. 1. Tomato plants after treatment for 28 days with 10 mg., 5 mg., 1 mg., and 0.5 mg. of TIBA. Control plant on left. 1/13 ×. FIG. 2. Tomato plants after treatment for 28 days with 0.5 mg., 0.1 mg., .05 mg., .01 mg., and .005 mg. of 2,4-D. Control plant on left. 1/13 ×. FIG. 3. Tomato plants treated for 28 days with 10 mg., 5 mg., 1 mg., 0.5 mg., and 0.1 mg. of B-naphthoxyacetic acid. Control plant on left. 1/13 ×. FIG. 4. Tomato plants treated for 28 days with 0.1 mg., .05 mg., and .01 mg. of N-1 naphthyl phthalamic acid. Control plant on left. 1/12 ×. FIG. 5. Two plants treated with TIBA, upper plant with 10 mg. and lower plant with 5 mg. (after 30 days) 1/10 ×. FIG. 6. Same as fig. 5. FIG. 7. Same as figure 5. FIG. 8. Smaller plant after treatment for 3 months with 2.5 mg. of TIBA. 1/3 ×. FIG. 9. Leaves of same age from plants treated with different concentrations of TIBA for 28 days. Upper row—control, 10 mg., 5 mg., and 1 mg. Lower row—0.5 mg., 0.1 mg., and .05 mg. 1/8 ×. FIG. 10. Leaves from plants treated with different concentrations of 2,4-D for 28 days. First column—control; second column—0.1 mg.; third column—.05 mg.; fourth column—.01 mg.; fifth column—.005 mg. 1/13 ×. FIG. 11. Top row—eight leaves of control plant, youngest on left; middle row—eight leaves of plant treated with 0.1 mg. of 2,4-D for 28 days; bottom row—eight leaves of plant treated with .05 mg. of 2,4-D for 28 days. 1/15 ×. FIG. 12. Top row—eight leaves of control plant, youngest on left; middle row—eight leaves of plant treated with 1 mg. of TIBA for 28 days; bottom row—eight leaves of plant treated with 5 mg. of TIBA for 28 days. 1/15 ×.

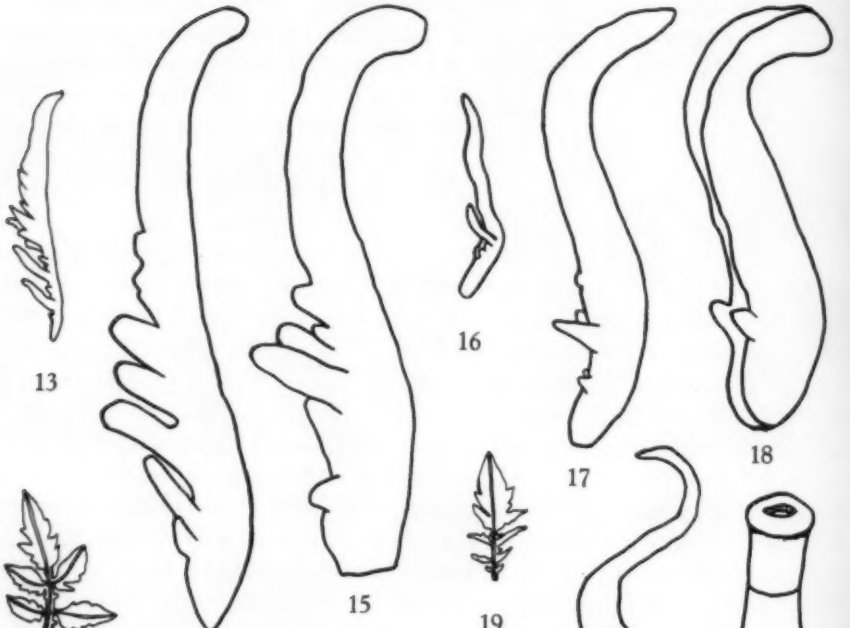
1951). The compound 2,4-D was chosen as the second treatment chemical mainly to enable comparison with other studies in which various plants were treated with 2,4-D and the effect on their leaves reported (Arvy and Lhoste 1947, Burton 1947 and 1950, Watson 1948, and Gifford 1953).

The major planting was commenced on April 17 with the sowing of over 3,000 seeds of *Lycopersicon esculentum*, Mill., var. Marglobe, in flats of garden soil in the greenhouse; 1,000 seedlings were individually potted in four-inch paper pots three weeks later. The seedlings chosen for potting were at the stage in which three true leaves were distinctly visible, and an attempt was made to select seedlings with similar growth rates. Seedlings with such morphological variations as three cotyledons, bifurcated cotyledons, and opposite leaves were excluded (Went 1943). Eight days later, on May 16, 900 plants in three lots of 300 plants each were treated using the lanolin block technique described above. Five mg. of TIBA in 125 mg. of lanolin were applied to the cotyledonary node of each plant in one lot, the second lot had 0.1 mg. of 2,4-D in 125 mg. of lanolin affixed to the cotyledonary node of each of its 300 plants, and 125 mg. of lanolin alone were attached to the cotyledonary node of each of the remaining 300 plants.

Starting with the day of treatment, daily collections were made of at least three plants from each lot for the first fifteen days. Similar collections were made every other day for the next twenty-seven days, and at three or four day intervals for the last twenty-eight days. The studies were terminated on the seventieth day after treatment had begun.

One plant from each of the three lots for each collection was dismembered under a binocular dissecting microscope, and camera lucida drawings were made of the stem apex and the leaf primordia. Leaf outlines of the mature and nearly mature leaves were traced and young leaves drawn freehand. Care was taken to avoid distortion resulting from water loss by placing the plant parts on moist filter paper while being examined under the microscope and by transferring the plant parts to the killing and fixing fluid as soon as possible after removal from the intact plant. Each stem apex and leaf primordium was individually killed and fixed using Randolph's modification of CRAF as described by Johansen (1940). Tissues were infiltrated with paraffin, using the t-butyl alcohol method of Johansen. Some embedded tissues were sectioned longitudinally and some transversely at thicknesses of 8–12 microns, mounted serially on slides, and stained with safranin O and anilin blue according to a modification of the procedure outlined by Popham, Johnson, and Chan (1948). For comparison some tissues were stained with tannic acid-ferric chloride and some with Feulgen.

Observations of normal shoot apices. The form of the vegetative shoot apex of Marglobe tomato is that of a convex dome (figs. 30 and 32). The mean diameter of the apices measured was 174 microns at the level of the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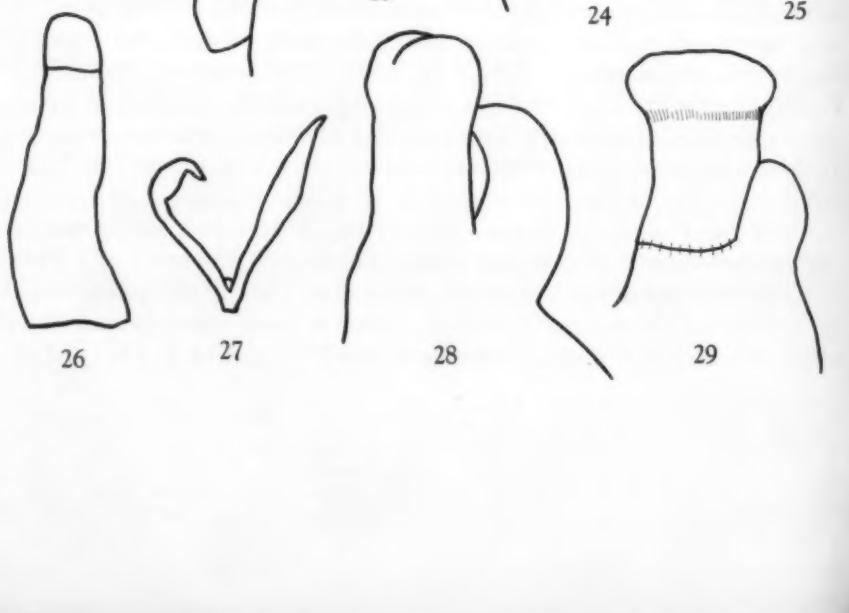
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most recently developed leaf primordium with a range of 110 to 270 microns. The mean height from the above level to the top was 70 microns with a range of 20 to 150 microns. Some variation in dimensions was related to the stage of the plastochron at the time of fixation. Apical meristems from older plants seemed in general to be of slightly greater dimensions than those of young plants. Leaf primordia develop individually and acropetally on the periphery of the apical meristem in a two-fifths spiral arrangement.

The histological structure of the apex consists of a tunica of two layers, in which all of the cells divide anticlinally with rare exceptions, and a corpus, in which divisions occur periclinally and obliquely, as well as anticlinally. Frequently the corpus shows stratification in its outer cells, particularly in some of the larger apices. This results in the appearance of two additional layers beneath the two tunica layers. These third and fourth layers are not considered to be part of the tunica, since they remain as discrete layers only temporarily and later show periclinal divisions, although not with the frequency of the innermost corpus cells. The cells of the second tunica layer in the main shoot apices of normal plants always divide anticlinally at the top but sometimes contribute to the bulk of a foliar buttress by one or several periclinal divisions toward the side. Periclinal divisions were never observed in the first tunica layer of normal plants grown in soil (figs. 30 and 32), nor, for that matter, in any of its epidermal derivatives, with the single exception of epidermal cells in an early phase of hair formation. In such instances, the division always results in an epidermal cell and an external cell, never an internal one.

In an ancillary experiment, however, in which small tomato plants were grown in an unaerated culture solution using the medium described by Taylor (1950) but without sucrose, vitamins, and casein hydrolysate, sev-

FIGS. 13–29. Camera lucida drawings of normal and modified tomato stem apices, leaves, and leaf primordia as seen under a dissecting microscope. FIG. 13. Eighth leaf of plant after 22 days of lanolin treatment. 2×. FIG. 14. Ninth leaf of plant after 22 days of lanolin treatment. 17×. FIG. 15. Tenth leaf of plant after 22 days of lanolin treatment. 35×. FIG. 16. Eighth leaf of plant after 22 days of TIBA treatment. 3.8×. FIG. 17. Ninth leaf of plant after 22 days of TIBA treatment. 17×. FIG. 18. Tenth leaf of plant after 22 days of TIBA treatment. 35×. FIG. 19. Seventh leaf of plant after 25 days of lanolin treatment. 0.5×. FIG. 20. Seventh leaf of plant after 25 days of TIBA treatment. 5.5×. FIG. 21. Ninth leaf of plant after 59 days of lanolin treatment. 0.5×. FIG. 22. Ninth leaf of plant after 59 days of TIBA treatment. 0.8×. FIG. 23. Cluster of cylindrical tips of plant after 22 days of TIBA treatment. 52×. FIG. 24. Axillary stem tip of fourth leaf of plant after 25 days of TIBA treatment. 35×. FIG. 25. Axillary stem tip of third leaf of plant after 25 days of TIBA treatment. 17×. FIG. 26. Axillary stem tip of third leaf of plant after 23 days of TIBA treatment. 35×. FIG. 27. Axillary bud of second leaf of plant after 25 days of TIBA treatment. Note spoon-shaped leaf on left. 5.5×. FIG. 28. Terminal stem tip of plant after 17 days of TIBA treatment. 52×. FIG. 29. Terminal stem tip of plant after 18 days of TIBA treatment. 52×.

eral periclinal divisions were seen in the first tunica layer toward the top of a single shoot apical meristem on a five-week-old plant. It is possible that this unusual event might have been induced by improper mineral nutrient balance or by oxygen deficiency.

The cells of the first tunica layer in most vegetative apices were distinguished from underlying cells by nuclei which absorbed the safranin stain more intensively and by the relatively large amount of tannin within their cytoplasm. In addition to the nuclei, the nucleoli of the first tunica layer in many apices appeared redder than those of the cells beneath. A number of apices also showed many nuclei of the first tunica layer (T1) lying next to the internal wall of their individual cells with a conspicuous vacuole separating them from the external wall. There is a strong possibility that this feature was a fixation artifact. In most apices the cells of the first tunica layer seemed to possess a somewhat greater amount of vacuolation or vesiculation than the underlying cells.

The tannin content of the T1 cells took the form either of diffuse material or of conspicuous tannin bodies of assorted sizes (fig. 30). The diffuse material in the cytoplasm was often localized about the nuclei, giving a pale yellow color to that region, whereas the larger tannin bodies, especially common in older plants, were more widely distributed through the cells. These latter tannin bodies, which in dehydrated tissues are described more accurately as particles of phlobaphene (the anhydrous form of tannin), were not found exclusively in the first tunica layer. Such inclusions were also abundant in developing pith and cortex at their early stages, as well as in the apical end and on the adaxial side of very young leaf primordia. They were relatively sparse in the second tunica layer and the corpus and were rarely found in the procambium. The developing epidermal layer, contrary to what might be expected, had a much lower tannin content than its originating layer, T1. To eliminate the possibility of these particles being fixation or dehydration artifacts, fresh tomato apices were sectioned by hand and examined in the living condition under the microscope. Some of these fresh sections were treated with 10% ferric chloride solution and some with 10% ferrous sulfate in 5% formalin as described by Johansen (1940). The untreated sections showed conspicuous, nearly colorless spherules in the aforementioned tissues, and the tests for tannin both produced positive, unequivocal results. Furthermore, tomato apices killed and fixed in basic fixation fluids of Zirkle, as also described by Johansen (1940), revealed an abundance of tannin bodies in the regions mentioned above.

One additional feature of the upper layer of the tunica was the distinctly greater height of its cells compared to that of the cells underneath. This added height plus the other distinguishing features of the first tunica layer suggested that a real difference in cell and nuclear volume might bear

a causal relationship to these T1 characteristics. Accordingly, measurements were made of the heights and widths of T1, T2, and corpus cells, and of the diameters of their nuclei. The cells of the first tunica layer had a mean height of 10.50 ± 0.22 microns, a mean width of 9.07 ± 0.31 microns, and a mean nuclear diameter of 6.03 ± 0.09 microns. The cells of the second tunica layer had a mean height of 9.28 ± 0.23 microns, a mean width of 9.50 ± 0.32 microns, and a mean nuclear diameter of 5.81 ± 0.15 microns. The cells of the corpus had a mean height of 9.74 ± 0.35 microns, a mean width of 9.56 ± 0.41 microns, and a mean nuclear diameter of 5.78 ± 0.10 microns. Calculations of the differences between the means of T1, T2, and the corpus revealed no statistically significant difference with the exception of the difference of the mean heights of T1 and T2 cells which, however, was highly significant. Indirect determination of the areas of these cells as seen in longitudinal sections indicated that the areas and, presumably, the volumes were not significantly different.

The cells of the second tunica layer could usually be distinguished from both T1 and corpus cells by the paler coloration of their cytoplasm.

Although mitotic figures were not usually abundant, those that were seen appeared to be distributed fairly evenly through the apical meristem. Close examination of cells in metaphase or anaphase did not uncover any observable difference in chromosome number of cells from different layers. Mitotic figures were also detected in the subapical region with nearly equal frequency.

Beneath the apical meristem, typical pith, procambium, and inner cortex differentiate from the corpus, while derivatives of T2 develop into the outer cortex, and T1 derivatives produce the epidermis. The procambial cells were distinguishable from those of both pith and cortex not only by their length and less vacuolate condition but also by the relative absence of tannin bodies which, as remarked before, were often relatively abundant in the early stages of pith and cortex development. There was generally a short zone of residual meristem between the apical meristem itself and the distinct procambial region.

The cell walls in the apex and below were characteristically thin, but there sometimes was some slight thickening, even within the apical meristem itself, at trihedral angles between contiguous cells.

The apical meristem of developing axillary buds is similar to that of the main shoot apex but smaller and usually without as pronounced a distinction between T1 and T2. It did, however, sometimes show several periclinal divisions in the second tunica layer toward the tip of the meristem.

The inflorescence apex, at the time of its initiation, arises from most of the main vegetative apex, leaving behind a portion of the latter in the

axillary bud position of the most recently initiated leaf primordium. This remnant of the original main apical meristem regenerates the entire vegetative shoot apex and outgrows the developing inflorescence which then assumes an apparently lateral position. Under the conditions of growth at the time of these studies the inflorescence apex generally developed after the initiation of the tenth true leaf. During the growth of the inflorescence apex, periclinal divisions were frequently observed in the position of the second tunica layer, while the outermost layer showed little of the red staining of the nucleus and of the accumulation of tannins characteristic of the first tunica layer.

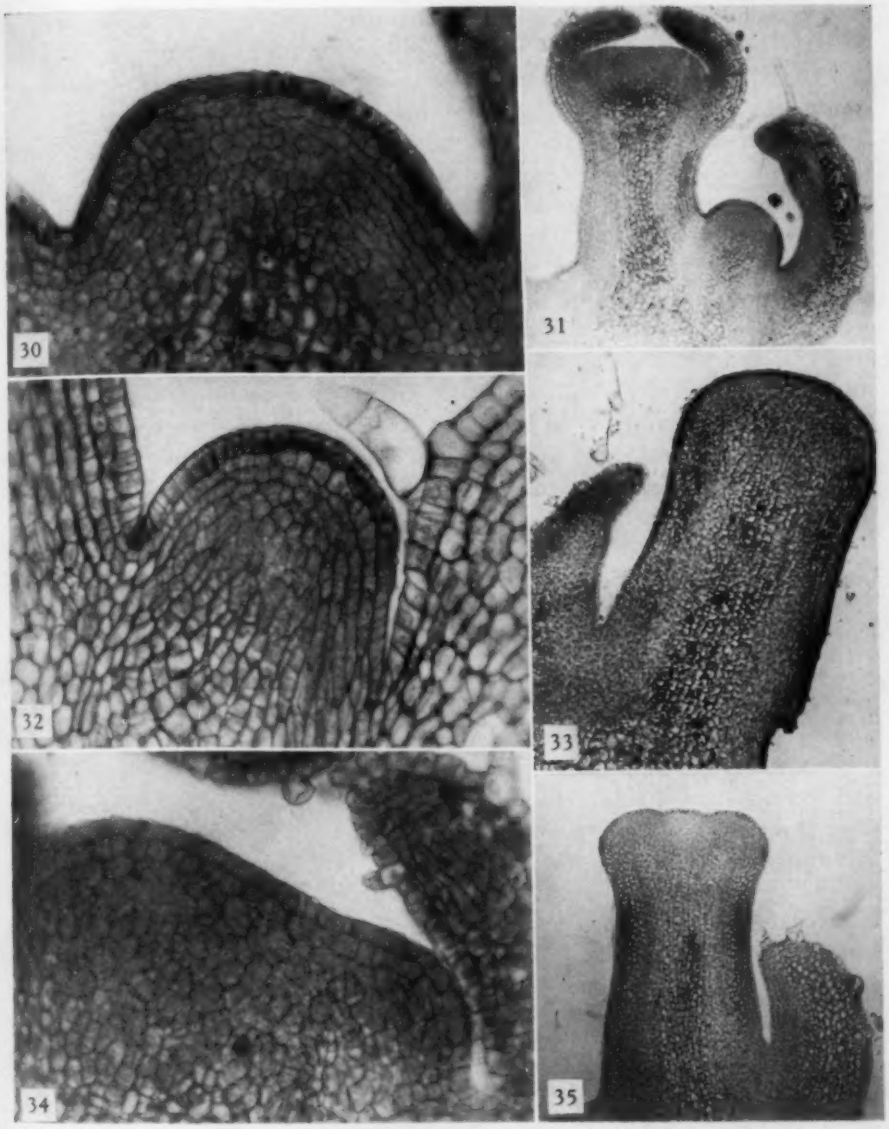
The inflorescence apex shortly after formation begins to initiate three and later more flower apices successively and in general basipetal direction. Each flower apex has, at its early stages, a slightly convex or flat apical surface with sepal primordia developing at the edge of this surface (figs. 31 and 34). The surface itself possesses an outermost layer of cells in which all divisions are anticlinal. This layer is analogous to the first tunica layer of the vegetative shoot apex except that in most cases it lacks the more intense staining of the nucleus and the conspicuous tannin bodies (fig. 34). Even before sepal primordia develop from the floral apex, this first layer of cells has lost most, if not all, of its stain differentiation, and tannin accumulation is reduced in amount or absent.

The nearly flat top of a flower apex with small sepal primordia generally showed some periclinal divisions in the second cell layer from the outside (fig. 34). Most second layer divisions though were anticlinal with the periclinal divisions confined to the peripheral areas of the flat disk of apical tissue in the presumptive positions of the later-forming petal primordia. In older flower apices, periclinal divisions occurred through most of the second outermost layer of cells including its center. Before sepal primordia originated, however, a few flower apices showed periclinal divisions, even in the center, in the second layer of cells from the outside. The meristematic layer of the flower apex is generally about six cells thick with the underlying cells showing noticeably greater vacuolation.

The axillary buds of the normal plants studied under the conditions outlined above never developed beyond the stage of having a small rounded dome with two young, relatively undifferentiated leaf primordia. Lateral buds in the axils of the first, second, and third leaves all seemed to be at the same stage of development in the oldest plants observed.

Comparisons of stem apices of Marglobe tomatoes with those of six other varieties revealed no fundamental differences in their apical architecture. Most of the varieties examined showed some difference of stain-take between the cells of the first tunica layer and their underlying cells.

Observations of modified shoot apices. The tomato plants treated with 2,3,5 triiodobenzoic acid and those treated with 2,4 dichlorophenoxyacetic



FIGS. 30–35. Photomicrographs of longitudinal sections of normal and TIBA-treated stem tips of tomato. FIG. 30. Normal main stem apex. 336 ×. FIG. 31. Normal flower apex and vegetative apex. Note difference between T1 layers of the two apices. 75 ×. FIG. 32. Smaller stem apex of normal plant. 336 ×. FIG. 33. Cylindrical stem tip of plant after 17 days of TIBA treatment. Gap on right is where a leaf primordium was removed. 110 ×. FIG. 34. Normal flower apex. Note the absence of darker nuclei and tannin bodies in the first layer and the presence of periclinal divisions in the second. 336 ×. FIG. 35. Stem apex of plant after 18 days of TIBA treatment showing a beginning ring. 68 ×.

acid responded initially in a similar manner. These responses consisted of severely bent stems near the site of application and epinastic leaves after two days in both sets of plants. The more permanent morphogenetic responses however were much greater in the TIBA-treated plants than in the 2,4-D-treated plants. The stem apices of plants with 2,4-D applications showed no shape change from the normal situation, although their mean dimensions were slightly smaller than those of untreated plants. The stem apices of plants with TIBA applications, on the other hand, developed radical alterations in form and structure. There was also a specific inhibition of leaf formation in these TIBA-treated plants. While 2,4-D, under the conditions of this study, inhibited normal growth and development generally, it did not seem to affect leaf primordium initiation in any special way. One remarkable result of TIBA treatment was the apparent inhibition of apical dominance as indicated by the accelerated activity and development of lateral shoot apices and of their leaf primordia. However, no new leaf primordia were initiated in axillary apices subsequent to the initial application of TIBA through almost the entire treatment period.

The plants treated with TIBA developed three basic types of modifications in their shoot apices: single, cylindrical structures with rounded tips (figs. 24, 26, and 33); single cylindrical structures with pronounced, funnel-shaped flanges at their tips (figs. 36, 37, 40, and 41); and a group of generally three cylindrical structures with rounded tips whose bases were situated at about the same position on the stem (figs. 23 and 39). The single, round-topped cylinders developed at the main apex early in the treatment period, and later at the lateral shoot apices. The single cylinders with funnel-shaped tips were sometimes found on the main stem generally after three weeks of treatment and more commonly in the axils of the third leaf and younger leaves after four weeks of treatment. The cluster of three finger-like projections, when present, occurred conspicuously after three weeks. Of the three types, the round-topped cylinder was most frequently formed, while the cluster of three round-topped cylinders was rarely found on the main stem and never found in axillary buds. In addition, many intergrading forms were observed which seemed to represent various stages in the development of each of the three general types or their ultimate differentiation as individual or clustered flower apices (figs. 25, 28, 29, and 35).

A bare cylinder was produced apparently because of the lack of initiation of new leaf primordia, as subapical tissues continued their growth and development mostly in the longitudinal direction. Axially oriented mitotic figures were observed in the middle and basal portions as well as in the upper parts of these columnar structures. In a number of cases, there were also divisions in the lower half which were oriented transversely, resulting in a greater basal diameter of these elongated tips. Consequently

such tips often appeared more conical than cylindrical (fig. 38). The more common cylindrical tips increased in length and diameter as growth proceeded; their average height at all ages on the main stem was over 600 microns, and their average diameter was a little less than 300 microns. The axillary cylindrical tips were often much taller and therefore appeared much leaner than the terminal ones; several as long as three and a half millimeters were observed.

The rounded top of the cylinder represented the persistent apical meristem which, however, was generally larger than in normal plants of the same age. The apical meristems in these, as well as in the other modified stem tips, continued to possess many of the features characteristic of unaltered apical meristems. Two usually distinct tunica layers were present with T1 cells showing the redder color and much greater concentration of tannin bodies, as seen in normal tomato plants. The cells of the second tunica layer retained their typically paler appearance. The cell walls in the apical meristem remained as thin as in normal apices. The walls sometimes developed slight thickenings at places where walls of three adjacent cells met, but this was also observed in the untreated stem tips. Two features observed in the modified apical meristems but not in the unaltered ones were the frequent occurrence of prominent vesicles in many of the meristem cells and the associated appearance of a shrinkage of the protoplasmic contents from their cell walls, leaving clear spaces between their membranes and the inner wall surfaces. It was not ascertained whether these phenomena occurred during the killing and fixing of these tissues or before, but, since cells of normal apical meristems rarely showed such vesiculation and shrinkage, it is assumed that their occurrence was dependent on vital changes in protoplasmic contents or properties. The cells of the first tunica layer in modified apical meristems were narrower at the sides of the meristem than on the top, indicating a greater rate of cell division on the periphery of the meristem. The distribution of mitotic figures tended to support this inference.

The cells of the outermost layer of the cylinder beneath the apical meristem generally occurred in vertical tiers. These cells were much thinner in the longitudinal direction than in other directions and thus had an appearance similar to that of a stack of bricks. Vertical tiers were also noted in the inner layers but were not nearly as conspicuous there as in the surface cell layer. Large tannin bodies were present in abundant amounts throughout the cylinder except for the cells of the procambium, the residual meristem, and T2 and the corpus of the apical meristem, in which they were virtually absent (fig. 39). The procambium had the form of a hollow cylinder with a thickness at any one point of approximately six cells. This procambium in all other respects was similar to that of normal tissue.

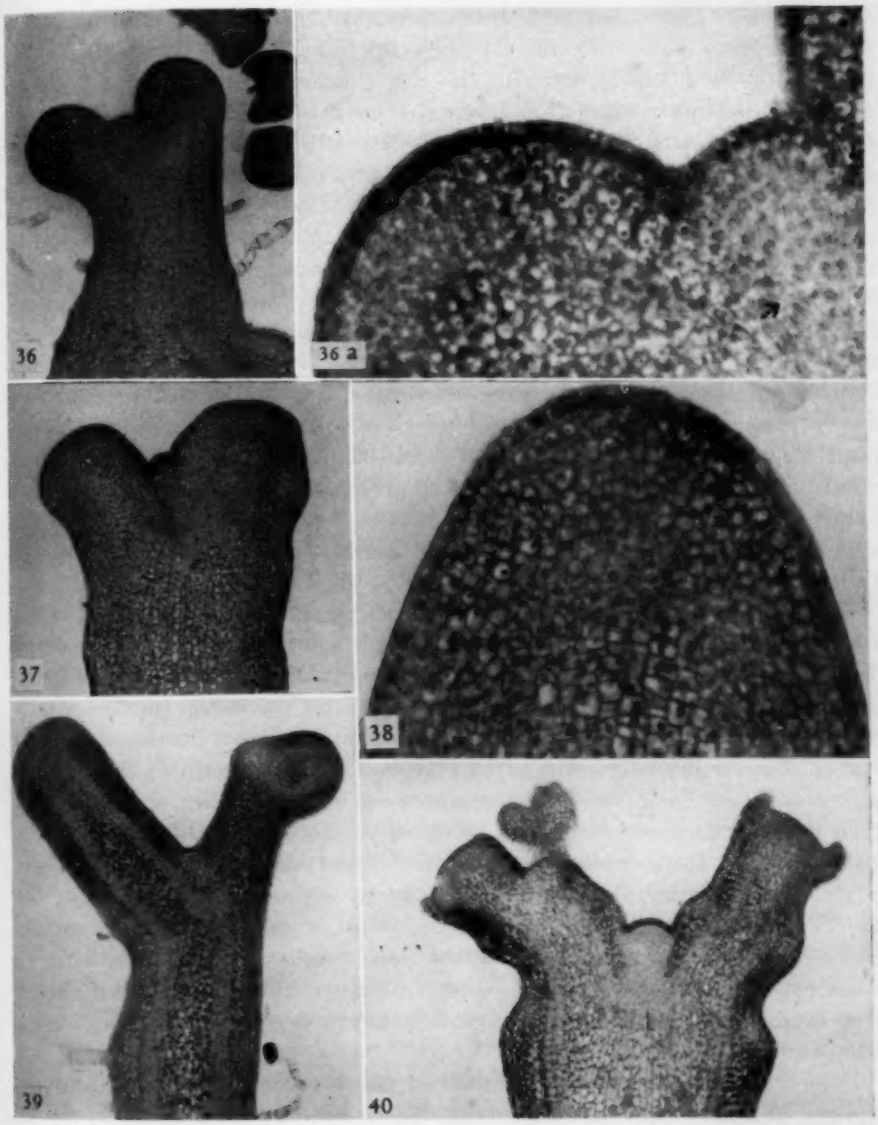
One feature of the cylindrical tip which was observed while examining

whole stem apices under the dissecting microscope was the presence of two zones distinguished by differences in intensity of green coloration. The upper zone, often about two hundred microns in length, was a much paler green than the lower zone, and the two zones were sharply separated, so that no transitional region existed. Examination of sectioned material with higher magnifications revealed the boundary between zones as being the location of an abrupt though slight increase in axis diameter. The cells external to the procambium below this line were conspicuously larger and showed greater development of chloroplasts than those above. This same feature was observed, though not described histologically, by Gorter (1951).

In some of the older cylindrical tips, some periclinal and oblique divisions were seen in the second tunica layer toward the side of the rounded apical meristem. This was true of both the main stem apices and the axillary stem apices. Other older cylindrical tips showed a circular swelling around the rim of the apical meristem forming a more or less regular ring surrounding the central surface (fig. 35). This ring-like protuberance apparently enlarged not only by outer divisions of the apical meristem flanks but also by cell divisions of the inner cells of the apical meristem.

This ring seemed eventually to proliferate a funnel-shaped mass of meristematic cells whose base encircled the remaining central apical meristem (figs. 25, 36, 37, 40, and 41). Such a proliferation is referred to in the literature as a ring fasciation. The central apical meristem was usually somewhat smaller than the apical meristem of normal plants and in later stages of ring enlargement and differentiation sometimes developed a slightly greater surface convexity. A curious feature of the tissue immediately surrounding the central apical meristem at the base of the funnel-shaped ring was the presence frequently of a layer of cells which appeared radially flattened (fig. 36A). This layer which surrounded the flanks of the central apical meristem was often not distinctly seen below this latter meristem. When continuous below the meristem, the layer resembled in three dimensions an hemispherical cup and seemed analogous to the transition zone described by Foster (1938) and Popham (1951).

The tissue of the central apical meristem differed from that of the distal meristem on the rim of the ring fasciation in three respects. One was the degree of general staining in the two tissues; the cells, particularly the cytoplasm, of the central apical meristem appeared much paler than the uniformly darker staining of the cells in the rim meristem (fig. 36A). A second difference was in the appearance of the cells of the first tunica layers in the two tissues. Although T1 cells from both regions showed marked accumulation of tannin bodies, those from the central apical meristem seemed to be redder, especially in their nuclei, than the ones on the rim of the ring. Actually, disregarding the large red tannin (phlobaphene) bodies which made both layers seem redder than their underlying cells,



FIGS. 36–40. Photomicrographs of longitudinal sections of TIBA-treated tomato stem apices. FIG. 36. Small ring fasciation at stem tip of plant after 29 days of TIBA-treatment. 68 ×. FIG. 36a. Central apical meristem of ring fasciation shown in figure 36. Note transition layer around central part (see arrows). 336 ×. FIG. 37. Small irregular ring fasciation at axillary stem tip of the third leaf from a plant after 30 days of TIBA treatment. Note darker T1 of control apical meristem. 75 ×. FIG. 38. Distal part of a conical stem tip of a plant after 21 days of TIBA treatment. 336 ×. FIG. 39. Two of three leafless cylindrical tips present on apex of a plant after 41 days of TIBA treatment. 75 ×. FIG. 40. Ring fasciation at axillary stem tip of the fourth leaf from a plant after 53 days of TIBA treatment. Note developing flower apices around rim of ring. 75 ×.

the cells and their nuclei of the first tunica layer in the central apical meristem were noticeably darker than the underlying cells, whereas the cells of the first tunica layer in the rim meristem were often not distinguishable in this regard from the cells underneath (fig. 37). The third difference was a more tenuous one; the T1 cells on the flanks of the rim meristem were generally, though not always, narrower than those on the flanks of the central apical meristem.

Procambial development in the ring fasciation proceeded directly with the enlarging ring. It started as a localized widening of the hollow procambial cylinder within the cylindrical stem tip just below the beginning circular protuberance. As the protuberance elongated to assume its characteristic funnel shape, it maintained meristematic connection with the central apical meristem by an inverted-cone-shaped layer of procambium and at the same time preserved connection with the procambium of the main stem by a similar, though larger, cone-shaped procambial layer. Somewhat later procambial connections were produced between the procambium below the central apical meristem and that of the main stem by an apparent development of provascular tissue from the relatively undifferentiated cells in its path.

Ring fasciations initiated localized areas of active meristematic growth from their rim meristems at either an early stage or sometimes much later. These localized meristems then developed in a characteristic way and produced special structures which indicated that they were fundamentally flower apices (figs. 40 and 41). The flower apices either started from the rim as discrete meristems, or, in a number of cases, a group of them began as a continuous bulge which later separated into a number of parts, each then developing as an individual floral apex. As a result of the latter sequence, flower apices were often seen in two partial or complete rings concentrically arranged along the outer edge of the ring fasciation rim (fig. 42). The continuous bulges around the fasciation rim, in a few cases, did not completely separate as individual flower apices, and consequently a monstrous multiple flower with a linear or ring-like shape resulted. In all ring fasciations observed, flower apices were the only structures to develop from the rim meristem.

The flower apex generally produced sepal primordia around the periphery of its flat or slightly convex apical meristem. The outermost cell layer of the latter apex contained abundant quantities of tannin bodies and had exclusively anticlinal divisions in its cells. Excluding consideration of the tannin bodies, these cells and their nuclei did not show a redder staining than their underlying cells. In this way they differed from the situation found in the normal apical meristem and in the central apical meristem of the ring fasciated plants. The younger flower apices on the ring rim sometimes displayed a few periclinal divisions in their second outer layer. The

older, flat apices usually had periclinal divisions in greater numbers in the same layer.

The flower apices from most of the ring fasciations studied had not neared maturity even at the close of the study; however, this may have been a secondary effect of the influence of TIBA on the general plant nutrition, rather than a primary effect on the floral apices themselves. Those flower apices that did enter the later stages of development initiated the characteristic flower structures in the usual sequence.

In the few cases where three finger-like cylinders developed in a cluster from the stem tip following TIBA treatment, their tips differentiated as single flower apices which went on to form small flower buds. Some single, cylindrical tips, instead of initiating a ring-like flange around their rounded tops, differentiated as a single flower apex or a cluster of flower apices without a central apical meristem. These floral apices seemed to follow the normal pattern in their early development.

Although all of the tomato plants treated with 2,4-D and not included in the stem tip collections had died by the end of the second month of treatment, most of the TIBA-treated plants which had not been killed and fixed for further study were still alive after seventy days. The few plants of this lot which had died were apparently the victims of tissue necrosis at the site of TIBA application. The majority of surviving plants, however, had apparently reached a state of equilibrium in which they were able to maintain themselves nutritionally but were unable to initiate new foliar organs and could produce reproductive organs and axillary meristems only sparingly. Growth in such plants had, therefore, nearly stopped.

There were at least a few plants which gave evidence of recovery from the effects of TIBA despite the fact that the lanolin block with TIBA was still attached to the side of the stem. Two such plants each possessed a newly formed leaf primordium on a very young axillary stem tip. Other plants displayed what seemed to be a slight renewal of growth.

The morphogenetic and histogenetic effects described above were probably not specific for this compound alone. An indication of this is that N-1 naphthyl phthalamic acid when applied to young tomato plants induced cylindrical stem tips much like the early ones induced by TIBA.

Observations of normal leaf primordia. The tomato leaf has its beginning as a foliar buttress upon the flank of the apical meristem. The buttress arises mainly as the result of periclinal divisions in the outer cells of the corpus, although cells of the second tunica layer make contributions to the developing bulge. Apical growth of the foliar buttress brings about the subsequent upward enlargement of the leaf primordium (fig. 31). This apical growth consists of exclusively anticlinal divisions in the outermost (epidermal) layer and regular periclinal or oblique divisions in the cell or cells of the subepidermal layer closest to the apex. Many divisions follow

in the immediate derivatives. The apical growth of the early leaf primordium is accompanied and followed by intercalary growth in the lower portion including periclinal divisions particularly on the adaxial side which add to the thickness of the primordium. The epidermis never contributes to the underlying tissues by dividing periclinally, and it thus remains as a discrete layer throughout the leaf at all stages of foliar development. The corpus of the tomato stem apex makes a substantial contribution to the basal portion of the leaf primordium axis.

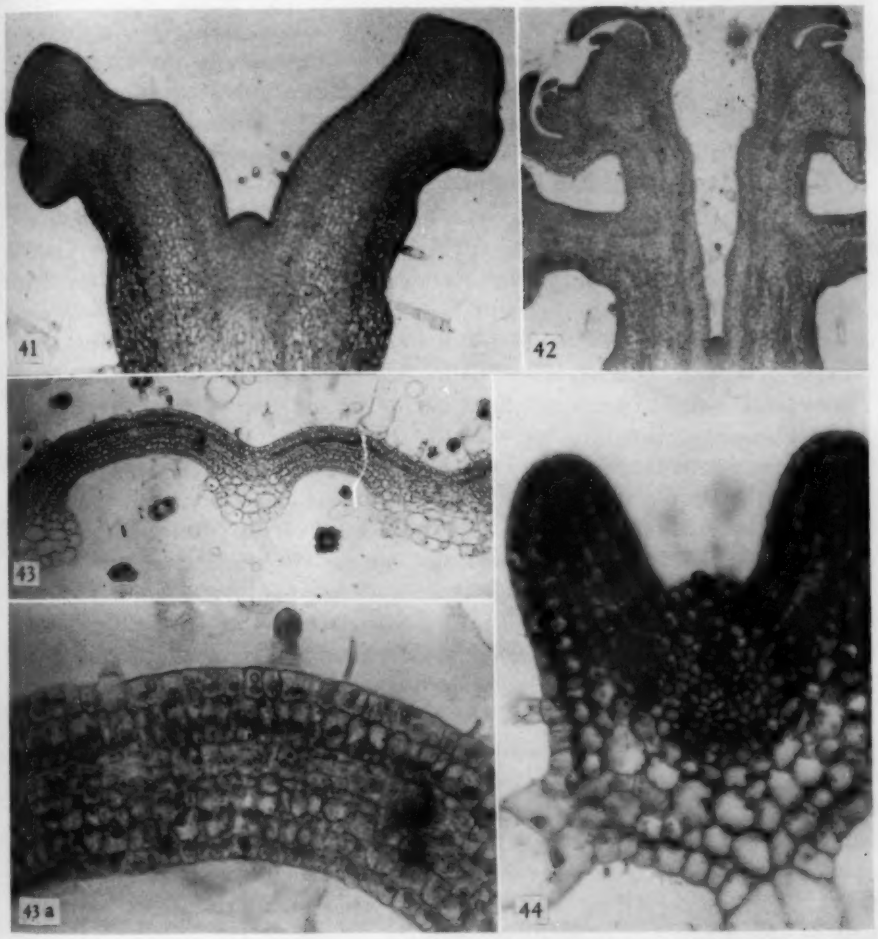
The mature leaf of young tomato plants is odd-pinnately compound with a terminal leaflet, generally two pairs of large lateral leaflets, and often two or more pairs of much smaller lateral leaflets between the larger ones (figs. 19 and 21). The first pair of large lateral leaflets are initiated as adaxial-lateral bumps about midway between the middle and the base of the leaf primordium when it is approximately 0.5–0.6 mm. long. As these protuberances increase in size and develop into leaflet primordia, intercalary growth in the main axis of the leaf itself intensifies, and, in so doing, carries the young leaflets-to-be farther away from the leaf axil. The second pair of main lateral leaflets develop as hemispherical mounds below the first pair when the leaf primordium is 0.7–1.0 mm. long.

Procambium differentiates as a continuation of the procambium of the stem into the base of the leaf primordium and in an acropetal direction within the primordium when it has a length of little more than one hundred microns. Xylem elements begin to differentiate in the lower half of the midrib procambium in leaf primordia of one millimeter length. Further xylem differentiation is both acropetal and basipetal from this place of origin. Phloem tissue starts its differentiation at about the same time or earlier, but its direction seems to be entirely acropetal from its origin within the stem. Procambium was distinguished in the first lateral leaflet primordium when it was 120–150 microns in length, and when the entire leaf primordium measured 0.8–1.0 mm.

When the embryonic leaf measures nearly 0.4 mm. in length, the lamina of the terminal leaflet is seen to begin its development on both sides of the entire distal half of the very young leaf. It is initiated on each side by a longitudinal row of subepidermal cells with their covering epidermal cells. These cells continue to add to the lateral extent of the lamina and are perpetuated for some time as a marginal meristem. Since their derivatives, in the main, divide anticlinally, they maintain the lamina at about the thickness originally determined by the marginal meristem. Later the lateral leaflet primordia develop a marginal meristem similar to that of the terminal leaflet lamina and at a comparable stage in their development.

Histogenesis of the lamina shows a fairly consistent pattern in all of the leaflets (figs. 44 and 46). The epidermal cells on the edge produce both the upper and the lower epidermis. The marginal subepidermal cells divide

anticlinally producing the adaxial and the abaxial subepidermal layers. They also act as submarginal initials in dividing periclinally and thus



FIGS. 41–44. Photomicrographs of longitudinal sections of TIBA-treated tomato stem apices and of transverse sections of normal tomato leaf primordia. FIG. 41. Ring fasciation at axillary stem tip of the third leaf from a plant after 40 days of TIBA treatment showing early stages of developing flower apices. 75 ×. FIG. 42. Portion of ring fasciation in axil of the third leaf of a plant after 70 days of treatment showing a well advanced developing flower apex. Central apical meristem is at lower right. 37 ×. FIG. 43. Young leaflet lamina. 68 ×. FIG. 43a. Portion of young leaflet lamina of figure 43 showing number and types of layers present. 306 ×. FIG. 44. Transverse section through terminal leaflet of young leaf primordium. 336 ×.

producing a strand of cells immediately behind the strand of submarginal initials. These deeper cells continue to divide for some time and in this way form a layer parallel to the surface, which is the third such layer from

the adaxial surface. Within this layer a number of individual cells divide periclinally two or three times, resulting in a short stack of cells perpendicular to the surface and no higher than the overall thickness of the layer itself. These cells, which develop in continuity with similar cells in the same layer, undergo further divisions and differentiate later as the lateral veins and veinlets of the leaf blade as reported by Lange (1927). The other cells in this third layer become the uppermost spongy mesophyll cells of the mature leaf. The abaxial subepidermal layer shortly after its formation (a cell or two from the submarginal initial) divides periclinally toward the interior to produce the fourth layer from the adaxial surface. The abaxial subepidermal layer is then the fifth layer from the top. The lamina thus has six layers at this stage. Somewhat later the fourth layer from the top often undergoes a further periclinal division thereby adding a seventh layer to the thickness of the blade (figs. 43 and 43A). These new fourth, fifth, and sixth layers eventually differentiate as spongy mesophyll. The adaxial subepidermal layer, at about the same time, rapidly increases in thickness by cell enlargement in the direction perpendicular to the surface. These resulting columnar cells later mature as the palisade mesophyll.

Differentiation of the leaf begins at the apical end when the primordium is about one millimeter in length. The process of differentiation includes differentiation of palisade and spongy mesophyll, development of xylem and phloem elements, and much later an increase in the amount of air space in the spongy mesophyll. This development proceeds basipetally through the entire terminal leaflet lamina. Similar basipetal differentiation occurs in the lateral leaflet blades. Xylem elements are conspicuous in the lateral veins toward the top of the terminal leaflet when the entire leaf primordium is little more than two millimeters long.

The mature leaflet lamina usually has seven cell layers in the area between veins. The lamina is noticeably thicker at the position of a major vein; this is partly the result of cell enlargement in the immediate vicinity of the vein and partly of an increase in the number of cell layers above and below the vein itself (fig. 43). The latter is noted particularly above the midrib vein where the adaxial meristem has persisted and formed a number of vertical tiers of enlarged, highly vacuolate cells. The ends of the veinlets on the mature blade margin usually have clusters of somewhat disoriented spiral tracheids. Trichomes are widely distributed in both epidermal layers. Many capitate hairs show rhombohedral bodies in the cells of their bulbous tips.

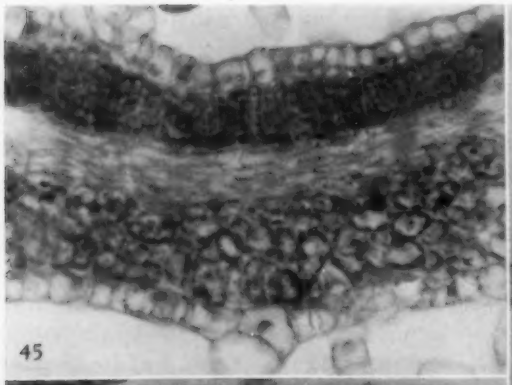
Observations of modified leaf primordia. Both TIBA and 2,4-D seemed to produce somewhat similar effects on the tissue development of leaves. Since TIBA, however, brought about more conspicuous alterations in leaf histogenesis under the conditions of this study, leaf primordia from plants

treated with TIBA were studied more intensively and will be the ones described in detail here.

As noted in the section on modified stem apices, one of the most striking results of TIBA treatment was the failure of the terminal apical meristem to initiate new leaf primordia. All leaf primordia that seemingly developed subsequent to treatment, with rare exceptions, were probably present as recently initiated leaf primordia at the time of TIBA application. Of the nine or ten leaves and leaf primordia found on the affected plants, the youngest were the most severely altered, and the oldest, the least. Specifically, the two oldest leaves often showed no noticeable difference in form or structure from the control plants (although sometimes the oldest leaves showed conspicuous modifications as in figure 12); the third leaf to develop was usually unaffected in the terminal and upper lateral leaflets but had slight modifications in its lower pair of lateral leaflets; the fourth leaf usually had all lateral leaflets altered on their margins with the terminal leaflet unchanged; and the five or six youngest leaves had all leaflets modified to some extent.

The affected leaflets on the third and fourth leaves seemed somewhat narrower with laciniate margins. The fifth leaf and all further leaves showed partial inhibition of rachis elongation and laminar expansion. This was much more pronounced in later developmental stages. In the earliest stages, the comparable TIBA-treated and normal leaf primordia were of approximately the same size. Lateral leaflets on young leaf primordia appeared long and narrow as a result of the reduction in laminar expansion (fig. 16). The terminal leaflet was sometimes also conspicuously narrowed. The lateral leaflet pairs were bent upward at their bases so that they lay parallel rather than in the same plane. In some cases, the youngest leaf primordia had one or both pairs of lateral leaflets poorly developed or absent (fig. 18). The lobing of the lamina in lateral leaflets was poorly developed or missing in the sixth and younger leaves. Lobing was also often poorly developed or absent in the terminal leaflets of the eighth, ninth, and tenth leaves (fig. 22). These and other abnormal features can be noted by comparing normal leaves and leaf primordia (figs. 13, 14, 15, 19, and 21) with TIBA-treated leaves and leaf primordia (figs. 16, 17, 18, 20, and 22) of the same ages.

The main histogenetic effects in leaves treated with TIBA were: (1) a general retardation of cell division and enlargement, especially at the later stages of development; (2) an increased development of procambium and resulting vascular tissue in the lamina (perhaps related to the first effect); and (3) a partial inhibition of centers of cell division and enlargement, as shown externally by the reduction in the number of leaflets and the amount of leaflet lobing. The earliest primordial development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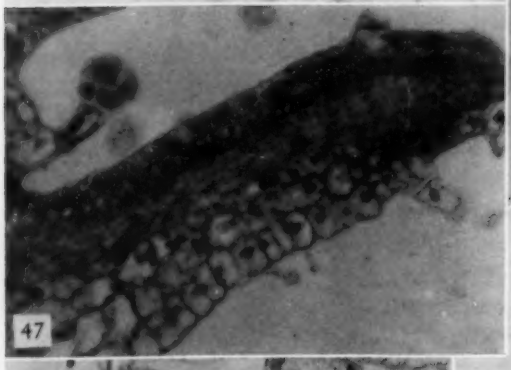
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apparently proceeded as in the normal plant. Petiole and midrib procambium differentiated acropetally and extended into the developing lateral leaflets. Lateral leaflets, when they developed at all, were initiated and enlarged at about the same time and in the same manner as in normal leaf primordia. Laminar construction by the marginal meristem followed the pattern seen in the normal leaf.

The increased procambial development in the leaflet lamina resulted in the formation of a continuous provascular layer, noticeably thickened in its early stages by the addition of many new cells (figs. 45, 47, 48, and 49). This increase in the number of procambial cells was brought about by many cambium-like divisions of all cells in the original layer. Such a continuous, multiple procambial layer was seen in young leaf primordia as early as one week after TIBA treatment was begun. This continuous procambial layer in the youngest leaf primordia appeared first in the upper part of the terminal leaflet. Somewhat older leaf primordia at the same number of days after the start of treatment exhibited normal vascular development at the upper end of the terminal leaflet, a continuous provascular layer in the middle part, and no conspicuous procambial differentiation in the lower part of the terminal leaflet other than at the midrib. Sections through procambial layers parallel to the laminar surface showed that procambial cells were without interruption within the area of the section. Similar parasections through the layer after spiral thickenings of differentiating tracheids had been formed revealed the same layer continuity (fig. 50). These cells often seemed to show orientation around certain points or "physiological centers" which seemed to be fairly evenly distributed.

In some cases, the parasections indicated that the above orientation was accompanied by an apical-basal orientation. When the continuous provascular layer in the terminal leaflet first showed xylem thickenings, each lateral leaflet generally had already developed a thick, uninterrupted layer of procambium in its apical part and sometimes below.

In an early stage, the differentiating adaxial and abaxial mesophyll frequently looked alike. This was enhanced, at times, by periclinal and oblique divisions in the adaxial layer. Often the nearly mature margin of a young leaf primordium had columnar mesophyll cells extending from the

FIGS. 45–50. Photomicrographs of transverse sections (and a parasection) of normal and TIBA-treated leaf primordia of tomato. FIG. 45. Leaflet lamina of an axillary bud leaf from a plant after 28 days of TIBA treatment. 336 ×. FIG. 46. Leaflet lamina of a normal young leaf primordium. 336 ×. FIG. 47. Leaflet lamina of the eighth leaf of a plant after 12 days of TIBA treatment. 306 ×. FIG. 48. Leaflet lamina of a young leaf primordium (Leaf 7) of a plant after 24 days of TIBA treatment. 75 ×. FIG. 49. Portion of a leaflet lamina of an axillary bud leaf from a plant after 22 days of TIBA treatment. Note the continuous vascular layer here as well as in figures 45, 47, and 48. 550 ×. FIG. 50. Parasection through continuous vascular layer of the sixth leaf of a plant after 17 days of TIBA treatment showing "scrambled" tracheids. 336 ×.

adaxial surface around the side to the abaxial surface in a continuous sheet. Tannin bodies occurred abundantly in the differentiating mesophyll and epidermal cells at their younger stages, especially along the edges and at the tips of the leaflet primordia. Such inclusions were small and few in number in the procambium and its derivative tissues or more often were apparently absent.

After about five weeks of TIBA treatment, some leaf primordia which were in the later phases of development showed a few gaps in the vascular layers of their blades. Similar leaf primordia which had been initiated at about the same time on the other treated plants had shown unbroken layers of vascular or provascular tissue at earlier stages in their ontogeny. At six weeks, the breaks in the vascular layer appeared more frequently and there was some indication that at least a few procambial cells might have been differentiating as mesophyll cells (that is, as cells with chloroplasts). In the mature and nearly mature leaflets, cross sections often revealed that the vascular tissue occurred as discrete patches separated by mesophyll areas of various widths. On the basis of the shapes and orientations of some mesophyll cells, it was inferred that the presumed continuous vascular layer might have been broken in part by the greater enlargement of the epidermal and mesophyll cells in planes parallel to the blade surface. Such gaps might have been filled by the adjacent expanding spongy mesophyll tissue. In some cases, the interrupting mesophyll cells were oriented in lines between vein elements in a way that indicated their possible origin from young procambium cells.

Leaves of axillary buds showed similar histological modifications following TIBA treatment, although their alterations were generally more extreme. There were usually three or four primordia on the lateral shoot apex in the axil of the first true leaf. They generally possessed slightly lobed terminal leaflets and only a single pair of narrow lateral leaflets per leaf. The youngest leaf in these oldest of axillary buds was often simple, with an unlobed, oval blade and a long petiole. The axillary stem tip of the second true leaf on the main stem had generally two or three leaves which were, in the majority of cases, like the two youngest leaves on the first axillary bud. The axillary stem tip of the third true leaf sometimes had one or two simple leaves, although in most cases no leaves occurred. These simple leaves, when present, and the youngest leaf on the second axillary bud bore unlobed, spoon-shaped blades with the convex surface on the abaxial side (figs. 8 and 27). The oldest axillary leaf primordia, such as the first leaf of the first axillary bud after three weeks of treatment, showed narrow, discontinuous vascular layers in their laminar tissue, with perhaps a slightly greater concentration of conducting tissue than in normal leaves. Younger axillary leaves seemed to have a more or less permanent layer of uninterrupted vascular tissue. The spoon-shaped leaves showed the most

severe modifications; namely, a fairly thick, continuous vascular layer and "replacement tissue" (Watson 1948) on either side. This latter tissue consisted of incompletely differentiated mesophyll cells with a few or no air spaces between them. The maintenance of a continuous layer of conducting cells in these leaves was probably related to the smaller size of the mature leaf blades. This was especially true of the spoon-shaped leaves which generally had blades not much longer than one centimeter.

The petiole of highly modified leaves had a more or less continuous vascular arc, which, in some cases, was ten or more cells thick. In the latter instances, the regular, vertical rows of cells indicated a cambium-like mode of origin. The xylem and phloem cells in their normal arrangement are accompanied by typical intraxylary phloem on the adaxial side, such as is found in the untreated tomato stem and leaf petiole. The petiole and midrib in older leaf primordia sometimes also developed collenchyma tissue on the adaxial side.

The younger leaves of plants treated with 2,4-D also showed a continuous provascular layer, though not as thick as in TIBA-treated leaf primordia. Some 2,4-D-treated leaves also possessed some replacement tissue near the midrib. A continuous procambial layer also developed in young leaves of tomato plants after treatment with N-1 naphthyl phthalamic acid or with B-naphthoxyacetic acid. These latter observations indicate that the development of the procambial layer was not specific for TIBA but was probably a more general one.

Discussion. The observation of two tunica layers in the shoot apical meristem of tomato confirms the findings of Steinberg (1950) and Gorter (1951). Lange (1927), on the other hand, reported four regular layers in the tomato stem apex. He observed though that periclinal divisions sometimes occurred in the third and fourth layers. His analysis is not inconsistent then with those of Steinberg (1950) and the author, both of whom observed two additional strata, at certain times, in the outer part of the corpus. Since these two layers were not constant, they should not be considered as part of the tunica. Schmidt (1924), who originally formulated the tunica-corpus concept, noted that the corpus (by his definition) often had its outermost cells arranged for a definite time in a noticeable layer but did not choose to interpret this in terms of a fluctuating tunica. Lange (1927) also studied interspecific periclinal chimeras resulting from grafts between tomato and *Solanum nigrum* and gave evidence that four discrete periclinal layers existed in several chimeras. This may, however, have little significance for tomato, since such interspecific periclinal chimeras probably had histological patterns of their own, rather than closely resembling either graft parent.

The cytological differentiation noted in a previous section was also reported in part by Steinberg (1950). He described the redder staining of

the T1 nuclei and the paler staining of the T2 cells. Several of his photomicrographs show this fairly clearly. Gorter (1951) made no mention in her paper of any difference between cells of T1 and the underlying cells in the normal stem tip, although her photomicrograph of a normal apical meristem showed T1 nuclei darker than the ones underneath. Steinberg (1950) stated that the nuclei of the T1 cells lie next to their internal cell walls with conspicuous vacuoles separating them from the external walls.

The ranges in dimensions of the apical meristem recorded here were greater than those reported by Steinberg (1950). This may be explained by the inclusion of older apices in the present measurements, since Whaley (1939) found that apical meristems of tomato generally increased in size as the plants enlarged.

Steinberg (1950) observed the greater height of the T1 cells and concluded that they were in general larger than the cells beneath. As reported above, the T1 cells measured in this study were significantly taller than other cells in the apical meristem, but determinations of mean cell areas in sections did not indicate a significant difference in overall size between T1 and other cells of the meristem. Whaley (1939) measured cell sizes in the apical meristem during its development, but he did not distinguish between tunica and corpus in these calculations.

Neither Steinberg (1950) nor Gorter (1951) reported observing any tannin bodies in the apical meristem, and their photomicrographs gave no indication of the presence of tannin inclusions similar to the ones observed here in the T1 cells of the older apical meristem. However, Steinberg (1950) mentioned a yellowish appearance in the perinuclear region of the cytoplasm which most probably was diffuse tannin material similar to that found in younger apical meristems of this study. Of course, it could very well be that the darker nuclei of the younger T1 cells mentioned before may have resulted from an accumulation of tannin material on or near the surface of the nuclear membrane. Collette and Gillette (1955) observed red-staining spherical bodies of various sizes in callus tissue which developed from the cut surfaces of decapitated tomato plants. These were most probably tannin bodies, although they did not mention this as a possibility. Cutter (1955) in observing enations on abnormal tomato fruits noticed many inclusions which were yellowish in color and which often contained numerous refractive granules. Comparisons of her published photomicrographs with observations of tannin bodies in normal and abnormal tomato tissues as described earlier strongly suggest that these bodies, which Cutter considered as possibly being virus X-bodies, were in reality tannin particles of normal occurrence in tomato. Ball (1950) made the suggestion that the presence of tannins might be incompatible with normal cellular activity in the shoot apex. This seems contrary to the observations here of abundant tannins in T1 cells of the normal shoot apical

meristem. Zirkle (1932) noted a large amount of tannin in the cells of the shoot apex of *Pinus strobus* dwarf shoots which were presumably in an inactive state. He also found in *Pinus* root tips an abundance of tannin in developing cortex and epidermis, as well as in the peripheral regions of the root cap, whereas the apical meristem, the procambium of the vascular cylinder, and the columella of the root cap seemed to be free of tannin inclusions. The distinct occurrence of tannin in the outer root tissues and its absence from the procambium is closely analogous to the situation in the younger stem of the tomato as reported above. Linsbauer (1930) described the common occurrence of tannins in the epidermis of many species. This was particularly true of the leaves, where it was often most concentrated in the upper epidermis, or the epidermis of the petiole or of the entire leaf blade. He also reported the accumulation of tannins in the epidermis of some stems. The localization of conspicuous tannin bodies in the first tunica layer of the shoot apical meristem has apparently not been previously reported in the literature.

Van Wisselingh (1910) summarized the knowledge up to that time of the physiological significance of tannins in plant bodies. The principal hypotheses were: (1) tannins are of no value to the plant, (2) they are excretory products, (3) they protect the plant against harmful external influences, (4) they contribute to the plant's metabolic processes, and (5) tannins can perform a number of different functions. Hauser (1936), on the basis of his studies of tannins in a gelatin-water-alcohol system, suggested that tannins played the role of a protective colloid in plant cells. Esau (1953) mentioned a number of other fairly specific hypotheses on the possible physiological actions of tannins, but it seems obvious that botanists are not much closer to a complete understanding of the function of tannins than they were in 1910. However, it seems plausible that the tannin present in T1 cells of the apical meristem may function as a protective colloid as Hauser suggested.

Comparison of leaf ontogeny in tomato with that in tobacco (Avery 1933) revealed that their developmental patterns were basically the same, with the exception of the derivation of some layers from the marginal meristem and, of course, the initiation of lateral leaflets on the tomato leaf. Beyond these differences, tomato leaf primordia enter a new phase of development generally when of a smaller size than tobacco leaf primordia. This latter observation might be correlated with the generally larger size of mature tobacco leaves.

There have been conflicting reports in the literature on the origin of the inflorescence apex in normal tomato plants. Cooper (1927) reported that the inflorescence axis grows from the axil of a leaf, whereas Muller (1940) and Zimmerman and Hitchcock (1942) stated that the inflorescence arises laterally from the stem opposite a leaf attachment or not associated

with a leaf. Muller did mention though that the inflorescence may, at times, be terminal in position. Venning (1949) characterized the inflorescence branch as arising from a dichotomous division of the stem tip. He wrote that a bifurcation of the main axis produces two main axes, one of which develops into the inflorescence, and the other continues as the vegetative axis. Went (1944) and Gorter (1949), on the other hand, described the normal inflorescence apex as being fundamentally terminal and developing from the vegetative shoot apex. Later, according to these authors, meristematic tissue in the axillary bud position of the most recently initiated leaf primordium grows out and subsequently outgrows the inflorescence apex. As a result, the inflorescence apex is pushed to a lateral position on the newly formed main axis. The observations of developing normal inflorescence apices in the present study agreed in every respect with those of Went and Gorter. If Venning's claim of dichotomy in the stem apex during initiation of an inflorescence were to be accepted, it certainly should be qualified with the comment that the bifurcation may be distinctly unequal even from the start.

The initial responses of tomato plants to TIBA or 2,4-D treatment were found to result in epinastic leaves and severely bent stems. Zimmerman and Hitchcock (1942) reported growth of odd curvatures on tomato stems following application of TIBA. Gorter (1949) mentioned leaf epinasty as one of the effects of TIBA on tomato. Prostration of tomato plant stems similar to the curvature effects reported here were observed by Ennis (1948) following O-isopropyl N-phenyl carbamate treatment.

The observations in the present study of cylindrical stem tips, terminal flower clusters on stalks, ring-fasciations, and fasciated flower primordia in tomato following TIBA treatment confirm the morphological findings of Zimmerman and Hitchcock (1942 and 1949a), de Waard and Roodenburg (1948), and Gorter (1949 and 1951). The tendency for tomato plants treated with TIBA to produce more axillary growth than normal plants was observed and depicted by all of the above workers as well as by the present study. This increased axillary development was probably brought about by an inhibition of apical dominance or, more specifically, by inhibition of auxin action at the apex or below.

The inhibition by TIBA of leaf formation in shoot apices of *Dryopteris* was reported by Wardlaw (1957a). Gorter (1949 and 1951) reported an absence of new leaf primordia on the main stem apices of TIBA-treated tomato plants, although she found a number of affected axillary stem tips with leaf primordia which had apparently been initiated after the application of TIBA. Under the conditions of the present study, no new leaf primordia were initiated on either main stem apices or axillary stem apices (with only two late exceptions) at any time during the course of

TIBA treatment. This nearly complete inhibition of leaf initiation on the entire plant may have been the result of the constant presence of TIBA in the affected tissues, since the TIBA-lanolin block was kept on the stem for the duration of the growth period. Gorter's treatment periods were generally of much shorter duration, and some of the axillary stem tips might have recovered in time to produce observable leaf primordia before her study was terminated.

The differences in modifications which developed in plants of the same age with the same treatment are explainable on the basis of slightly different growth rates and therefore also slightly different stages of ontogeny. Since the plants at the time of treatment were apparently close to or at the stage of inflorescence apex initiation, a slightly more rapid growth rate might have resulted in plants having their inflorescence apices or even individual flower apices already present at the time that TIBA was first applied. If individual flower apices had even begun to form before treatment, then each one might have formed its own elongated stalk. This may be tentatively accepted as the explanation for the occurrence of three clustered cylindrical tips on a few treated tomato plants. Many other special types of modifications which were infrequently observed can probably be explained in a similar way. Zimmerman and Hitchcock (1949a) and Gorter (1949) both remarked that there was a definite direct relationship between the growth rate of the plants and the effects of the chemical. One corollary to this, which was noted by the present writer, is that the younger the plant was at the time of treatment, the more easily and radically it was modified by the chemical. This latter statement, if true, would explain the much more pronounced alterations found by de Waard and Roodenburg (1948) after treating tomato plants with TIBA only six days after sowing.

The leafless cylindrical and conical tips, which were among the first of the stem apex modifications to develop, had a superficial resemblance to the elongate, cone-shaped apical meristems of such angiospermous aquatic plants as *Anacharis*, *Hippuris*, and *Hydrocharis*. However, the two types differ in several fundamental ways. Firstly, the TIBA-induced cylindrical tips had no leaf primordia arising from anywhere on their surfaces, whereas the stem apices of the aforementioned aquatic plants have very young buttressless leaf primordia forming low on the apical cone. A second and much more important difference is in the meristematic nature of the two types of tips. The cylindrical tips of TIBA-treated tomato plants showed true apical meristem only at their rounded tops with the underlying cells showing differentiation as the three primary meristematic tissues of protoderm, procambium, and ground meristem; the entire conical apex of *Anacharis* and similar aquatic plants consists of apical meristem alone.

Also, TIBA-induced cylindrical tips of tomato main stems were, on the average, almost three times as long and more than twice as wide as the typical *Anacharis* stem tip measured above the first visible lateral primordium. A further difference was in the number of cells determined in both dimensions in the two groups. Matzke and Duffy (1955) in studying cell shapes in thousands of *Anacharis* shoot apices found that the apical meristems averaged 9–13 cells in diameter and approximately sixteen cells in length, while early cylindrical tips of tomato were estimated to have been about 27–30 cells wide and 46–50 cells high. In a study of the distribution of mitotic activity in the shoot apical meristem of *Elodea* (*Anacharis*) *densa*, Savelkoul (1957) found that the distal end had a conspicuously lower rate of mitotic activity than the more proximal portions of the apex. In this regard, *Anacharis* resembles the TIBA-modified cylindrical tip of tomato with its partially inhibited apical meristem.

Claes (1952) found that the vegetative shoot apices of *Hyoscyamus niger* following TIBA treatment developed into elongated conical apices with ridges around the surfaces of the cones. These ridges were interpreted as leaf primordia which had been strongly inhibited in their development. Claes stated that the elongation of the axis to form a conical tip resembled the axis elongation which occurs simultaneously with flower formation in *Hyoscyamus*, but that the plants nevertheless remained clearly vegetative. Although it is possible that these conical tips were strongly inhibited inflorescence apices, it is more likely, on logical grounds, that they were analogous to the leafless cylinders of treated tomato plants except that their leaf primordia were not as completely inhibited.

In her anatomical studies of TIBA-modified tomato stem apices, Gorter (1951) reported observing noticeably thick walls in the cells of the apical meristem and a single tunica layer rather than the typical two tunica layers of normal tomato plants. Neither thick cell walls nor a clearly single tunica layer could be found in tomato shoot apical meristems modified by TIBA under the conditions of this study. However, Gorter's photomicrograph of a TIBA-treated shoot apex closely resembles sectioned apical meristems observed by the author in which there was an obvious shrinkage of the protoplasmic contents within the cell walls as reported previously. It is possible that Gorter might have interpreted the clear spaces between the protoplasmic membranes and the cell walls as being much thickened hyaline walls. It is also conceivable that differences in the two experimental techniques and in the tomato varieties used might account for both discrepancies. The second tunica layer observed in this study did show some periclinal divisions on the periphery of the rounded top during the apparent initiation of the ring from the cylindrical stem tip. The apical meristem during this stage might then be described as having only one tunica layer.

It should also be mentioned that Ball (1944) reported a temporary reduction in the number of tunica layers from two or three in the normal shoot apex to one layer in the affected shoot apex of *Tropaeolum majus* following applications of indoleacetic acid or indolepropionic acid emulsions to the apical meristem itself.

In a study of the effect of gamma irradiation on shoot apices of tobacco, Crockett (1957) found many periclinal divisions in the topmost cells of the first layer of the normally two-layered tunica while T2 had completely lost its identity as a distinct layer. These observations in tobacco, as well as those of Crockett in irradiated *Coleus*, support the author's findings in tomato that the deeper a layer is in the apical meristem the more easily is its plane of division disturbed by abnormal stimuli. In tomato, for example, the third layer is somewhat more distinct than the fourth layer, the two tunica layers are much less alterable than the two temporary layers of the corpus, and T2 has an increasing number of periclinal divisions after TIBA treatment, while the divisions of T1 remain solely anticlinal.

The development of ring fasciations in tomato following TIBA treatment, as described in the section on modified stem apices, was first observed by Gorter (1949 and 1951), although de Waard and Roodenburg (1948) apparently saw young ones without recognizing them as such. Zimmerman and Hitchcock (1949a), judging by their descriptions and photographs, probably also saw such malformations but did not distinguish them as ring fasciations. The ring was seen in the present study to develop as a continuous bulge around the circumference of the cylindrically modified stem apex at its top. In a few instances, the beginning ring was incomplete, so that it looked from a top view like the letter C. Consequently, ring fasciations developing from such incomplete circular mounds had gaps or openings in their sides. Some of the peculiarly modified stem tips, such as the "ball and mitten" apex, observed and depicted by Gorter (1951, Plate I, 16D), may be explained on the basis of such sectorial development of the incipient ring. Gorter (1951) reported mostly flower apices but by implication also leafy vegetative apices on the rim of the fasciation. In the present study only floral apices occurred on the ring. Possibly the meristematic tissue in the ring fasciations of her study had recovered sufficiently after the termination of treatment to be again capable of leaf initiation. Since TIBA treatment was uninterrupted during the entire time that living plants were being observed here, there was neither a renewal of leaf initiation at the ring-fasciated stem tip nor a renewal of growth at the central apical meristem within the ring fasciation such as was reported by Gorter (1951). Both Gorter (1951) and Wardlaw (1953) described the vascular anatomy of the mature ring fasciation. They observed cross-sections through the funnel-shaped fasciation and stated that it possessed

two concentric, continuous vascular rings separated by pith parenchyma. The outer vascular ring showed the normal orientation of xylem and phloem, while the inner ring showed these tissues inversely oriented.

Ring fasciations, especially during their initiation and development, can be compared in several aspects to the "anneau initial" (initial ring) of Plantefol (1947) and Buvat (1952). Firstly, the beginning ring of tomato and the "anneau initial" as described are in similar positions within their stem apices. The "anneau" as a place where centers of future leaf primordia are organized also resembles the physiological and morphological pattern of the early tomato ring fasciation. However, the homology of the two structures is highly questionable. The ring seemed to include much deeper tissues than the "anneau initial." Under the conditions of this study, the tomato shoot apex does not show the distinctive stain differentiation in the position of the proposed "anneau" which is so clearly shown in the normal tobacco shoot apex (Crockett 1957). If the "anneau" is a strictly morphological entity, then it is apparently absent from tomato. In a synthesis of observations and views on the apical meristem, Wardlaw (1957b) cautioned the proponents of the "anneau" for their overemphasis on the seeming inertness or inactivity of the most distal region of the meristem. However, at least one interpretation of the results described here with tomato supports the above position taken by Buvat (1952) and his colleagues.

Gorter studied one hundred plants grown from seeds of ring-fasciated inflorescences and did not find a single ring-fasciated stem. She concluded that these ring fasciations were not inherited. Studies of fasciations in certain genetic stocks of tomato (Zielinski 1948 and Mertens and Burdick 1954) indicated though that some tomato fasciations are induced genetically. White (1948) pointed out in his review of the literature on fasciations that the common commercial varieties of tomatoes all represent degrees of fruit fasciations as shown by the increase in their locule number over the normal two.

Savelli (1927) described certain ring fasciations and other fasciations of tomato flowers. He concluded that they were evidently derived from lateral invaginations. His diagrams and descriptions of ring-fasciated flowers show the close resemblance of them to the TIBA-modified flower with a ring-shaped ovary as shown in a photograph published by Zimmerman and Hitchcock (1949a, Figure 1c).

In his general discussion of ring fasciations Nestler (1897) gave three possible explanations for the origin of the ring: (1) it may be formed by a growing together of several hypothetical growing points, (2) it may result from peculiar divisions of an apical cell giving rise to cells lying in a circle, and (3) it may develop from actively growing meristematic tissue

around the apical meristem following stoppage of growth in the apical part of the latter tissue. Nestler also proposed that the instances of rings forming as fusion products, as in (1) above, be designated connations rather than true fasciations. Gorter (1951) concluded from her studies of the TIBA-induced ring fasciations that they resulted from a growing together of several apices and therefore could be considered connations rather than fasciations in the narrow sense. She apparently based this upon the observation of discrete meristematic centers of growth around the rim of the ring fasciation. Wardlaw (1953) pointed out that some ring fasciations did not have this latter feature and took a contrary stand that the ring fasciations may have developed from actively growing tissue at the periphery of the apical meristem. He hypothesized that recovery from the effects of TIBA treatment would permit the meristematic cells of the ring to initiate a number of small buds around its rim. As described earlier, observation of the ring tissue at many stages of its development presented strong evidence that the ring fasciation developed from peripheral tissue of the apical meristem. It could not be considered to result from a fusion of growing points unless such hypothetical growing points were assumed to be physiologically discrete but morphologically unrecognizable. It is likely that the meristematic growth centers around the ring fasciation rim which Gorter observed were recently initiated flower apices. Such flower apices were found in the present study to occur in later stages of development in the ring fasciation during continued TIBA treatment. In a study of certain genetically controlled stem fasciations in tomato, Mertens and Burdick (1954) concluded also that ring fasciations resulted from a modification of a single apical meristem and were not the result of fusion of several meristems.

A further point of possible disagreement is the fundamental morphological and physiological nature of the tissue making up the funnel-shaped ring. Is it essentially cauline in nature, or is it actually a foliar structure incapable of differentiating in the normal way? It would seem on the basis of the morphological evidence that the ring itself is fundamentally a modified stem structure.

A number of papers describing the morphogenetic effects of various organic compounds on leaf formation have appeared in the literature. Arvy and Lhoste (1947), in reporting morphological anomalies induced in tomato plants by the sodium salt of 2,4-D, mentioned the reduction in size and blade expansion of affected leaves, as well as their distinct hyponasty. They did not, however, examine the internal structure of the modified leaves. Burton (1947) and Watson (1948) described the formative effects of 2,4-D on bean leaves and both noted the great increase in relative amount of vascular tissue in the developing leaves following treatment.

Burton stated that chlorenchymatous tissue was confined to the margins of leaves treated with 2,4-D or with 4-chlorophenoxyacetic acid. Watson concluded that much of the distortion of leaves was brought about by the development of "replacement tissue" and by the failure of normal laminar expansion with a consequent occurrence of many closely placed veins. Burton (1950) and Gifford (1953) described the histogenetic responses of developing cotton leaves to 2,4-D treatment. Both authors reported extensive amounts of vascular tissue in the most radically affected leaves which resembled the alterations induced in bean leaves by the same chemical. Their analyses of the pattern of marginal growth in the leaf of the untreated cotton plant showed a close similarity of this laminar growth pattern to that of the untreated tomato leaf described in the present study. An additional feature noted by Gifford in the developing cotton leaf following 2,4-D treatment was the occurrence of many more periclinal divisions in the cells of the middle laminar layer (procambium layer) than was found in normal laminar development. This, coupled with the partial inhibition of mesophyll development, of leaf lobing, and of laminar expansion, accounted for the continuous layer of vascular tissue occurring in the most severely modified, strap-shaped cotton leaves. Wangermann and Lacey (1953) reported an increase in the number of veins in *Lemna* fronds following TIBA treatment. Whereas the normal frond had only three or four veins, the treated frond developed five or more veins. The non-vascular tissue was apparently unaffected. The three plants mentioned above (bean, cotton, and *Lemna*) and tomato plants had in common then an increased development of vascular tissue after exposure to 2,4-D or TIBA.

Coalescence of leaves (connation of leaves) has been reported by workers in a number of plants following treatments with one of several growth-modifying substances. Coalescence of leaves resulting in the formation of a cone-shaped cup occurred on *Kalanchoe daigremontiana* after treatment with TIBA, 2-chloro-3,5-diiodobenzoic acid, 4-chlorophenoxyacetic acid, or certain phenoxy acid derivatives (Zimmerman and Hitchcock 1949b). Similar cone-shaped cups, presumably of leaves with fused margins, were described by von Denffer (1951) in *Kalanchoe Kirkii, Kalanchoe Blossfeldiana, Hydrangea scandens*, and three decussate species of *Penstemon* following TIBA treatments. Rüdiger (1952) treated flax plants with the sodium salt of 2,4-D and described the tubular connations of apparently fused leaves which subsequently developed. The remarkable resemblance between these leaf connations and the TIBA-induced ring fasciations of tomato leads to the consideration that they might be fundamentally the same sort of structure. However, von Denffer's illustration of a cross-section through a cone-shaped cup seemed to show that the vascular tissue was typically foliar in its distribution, whereas older tomato ring fasciations

showed two concentric vascular rings in a pattern that would be expected in an hypothetical apically invaginated stem. In addition, transitional forms indicated that connations were fundamentally fused leaves and that ring fasciations of these studies were modified cauline structures.

With the report of Zimmerman and Hitchcock (1942) that TIBA furthered flowering in tomato by increasing the number of floral apices formed from vegetative tissue, many studies were initiated in an attempt to verify this effect in other plants. Most of these workers reported that TIBA increased the number of flower apices present once flowering had started, but apparently it was not able to bring on flowering if the plants were growing under normally vegetative conditions. Galston (1947) found after treating soybean plants with TIBA that although this compound showed no florigenic effects it stimulated a greatly augmented number of flower apices to be formed after flowering had commenced. Von Denffer (1950) treated sixty-four species of plants with TIBA and later stated that, except for tomato, none of these species showed any indication of flower induction as a result of the TIBA treatment. Gorter (1951 and 1954) found that TIBA treatment increased flower production of tomato plants and bean plants, although it did not seem to induce the onset of flowering. The present study agrees with these findings in tomato.

Many papers have been published in recent years on the physiological action of TIBA and other growth-modifying compounds in plants. Only those papers will be reviewed here which seem to have direct bearing on the interpretation of this study. Kuse (1953), after studying TIBA and indoleacetic acid (IAA) relationships in excised pieces of sweet potato stems, concluded that IAA was probably blocked or inactivated at the part of a petiole which had been treated with TIBA. Hay (1956) showed further that translocation of IAA through excised sections of stems and roots of bean seedlings was inhibited by pretreatment with TIBA or 2,4-D. These findings indicate that the effect of TIBA on plants may not be a direct one. It is more likely that at least one of its general effects is probably to inactivate, or to inhibit the transport of, the plant's native auxin. Since auxin production in tomato plants apparently increases with age (Kramer and Went 1949), the greater response of younger tomato plants to small amounts of TIBA might be partly explained by the antiauxin effects of TIBA mentioned above.

Åberg (1953) found that at very low concentrations TIBA acted as an auxin synergist, at somewhat greater concentration it acted as an auxin antagonist, and at high concentrations TIBA caused a growth inhibition which was probably not specifically related to the auxin mechanism. These differing effects of different concentrations of TIBA might help explain

why TIBA has such variation in its morphogenetic effects even within a single plant.

Another possible physiological explanation for certain specific effects of TIBA is that it might interfere in some way with the normal action of some leaf growth factor present naturally in the plant. Other specific effects of TIBA on the aerial parts of tomato plants might possibly result indirectly from the inhibition of root development, for it was noted that some TIBA-treated plants seemed to have a less well developed root system than normal plants.

Applying the principle of Occam's razor, it seems most plausible that the enhanced flower formation was a direct result of the leaf inhibition; that is, the meristematic tissue at the shoot apices, with all leaf formation inhibited, might have differentiated in greater numbers into the only other relatively independent, determinate organ normally produced by the plant, namely the flower.

The basic nature of the vegetative apex and of the reproductive apex has been considerably discussed in recent years (Gifford 1954). Comparisons of vegetative apices and flower apices in TIBA-treated tomato plants revealed certain similarities as well as differences. A particularly conspicuous cytological similarity was the presence of larger tannin bodies in the first cell layer of both apices (the first cell layer of the normal flower apex did not contain this feature). This could be interpreted as an indication that the two types of apices are not fundamentally dissimilar.

SUMMARY

1. The normal shoot apical meristem of tomato was found to have the form of a convex dome with two tunica layers as previously reported. The cells of the first tunica layer were distinguished from underlying cells by nuclei which absorbed the safranin stain more intensively and by the relatively large numbers of tannin bodies in the cytoplasmic portions of their cells. Tannin bodies were also found in subjacent differentiating tissues with the exception of the procambium.

2. The first cell layer in the developing normal flower apex differed from the first tunica layer of the shoot apex in the absence of special staining properties and of conspicuous tannin bodies.

3. The plants treated with 2,3,5 triiodobenzoic acid (TIBA) developed three basic types of modifications: single, cylindrical structures with rounded tips; single, cylindrical structures with pronounced, funnel-shaped flanges at their tips; and groups of generally three cylindrical structures with rounded tips. Many intergrading forms were also observed. All of these structures almost invariably initiated flower apices at their apical ends.

4. The funnel-shaped flanges on certain modified stem tips often eventually developed into conspicuous ring fasciations with their bases encircling persistent, though inactive, central apical meristems. The beginning flange, or "ring," apparently enlarged by additions of new cells from both outer and inner meristematic tissue.

5. Development of normal leaf primordia of tomato followed the typical angiosperm pattern. The leaf at first produced only a single terminal leaflet but later initiated an upper pair of lateral leaflets and subsequently another pair below the first. The mature leaflet lamina was produced by a marginal meristem and generally possessed seven cell layers. The veins and veinlets in the leaf blade developed mostly from the third laminar layer.

6. No new leaf primordia were initiated at tomato stem apices during TIBA treatment with a few rare exceptions at a late phase of the study. The youngest leaf primordia present at the time of treatment showed the following main histogenetic alterations: (a) a general retardation of cell division and enlargement; (b) an increased development of procambium in the lamina; and (c) a partial inhibition of centers of cell division and enlargement, as shown externally by the reduction in the number of leaflets and the amount of leaflet lobing. The heightened procambial development usually resulted in the formation of a continuous vascular layer. This tissue often did not persist as a continuous layer as the leaf matured.

7. Morphological and physiological aspects of TIBA-induced modifications of tomato are discussed, including the nature of the induced ring fasciations. These rings are interpreted as cauline structures which developed from meristematic tissue in the apical meristem following inhibition of growth in its most apical part.

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BULLETIN OF THE TORREY BOTANICAL CLUB
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DE BARY BUBBLES IN ASCOSPORES OF SORDARIA FIMICOLA

LINDSAY S. OLIVE

At the request of Dr. B. O. Dodge, whose recent paper on this subject appeared in this journal (1957). I have applied to *Sordaria fimicola* his technique for producing de Bary bubbles in ascospores and am submitting this note containing my observations on these structures.

When Shear's Mounting Fluid (SMF) is added to clusters of mature asci of *S. fimicola,* de Bary bubbles appear very readily in the ascospores, as described by Dodge for other ascomycetes. These bubbles reach full size within about a minute after SMF is added, at which time they generally extend across the breadth of the spore, bounded by the inner walls. A single bubble appears in each spore. Spores dried in the air very quickly develop similar bodies. These bubbles undoubtedly add to the buoyancy of the spores as they are discharged from the asci. When spores dried in air or treated with SMF are returned to water, the bubbles disappear in a minute or so. If the spores are again transferred to SMF the bubbles reappear.

The components of the mounting fluid (glycerine, alcohol, potassium acetate in aqueous solution) either do not enter the spores or do so in non-toxic concentrations, for spores transferred to water and then to agar after several minutes in SMF germinate readily.

When hybrid asci containing four gray and four wild-type ascospores are placed in SMF, de Bary bubbles appear only in the wild-type spores, while the gray spores collapse (fig. 1). The latter, which normally germinate somewhat earlier than wild-type spores, probably have less resistant walls. Immature spores, like the gray ones, fail to form de Bary bubbles.

There has been some question among observers as to the nature of these structures within treated spores. Since the present experiments have shown them to be decidedly of a gaseous nature, I have not hesistated to call them bubbles. They have the characteristic dark periphery and light center. But even more convincing is the fact that when pressure is firmly applied to the cover slip so as to crack the spore walls, the bubbles may be forced out into the mounting fluid where they disappear at different rates, some within a few seconds after being pressed out, the majority within a minute. Some larger ones formed by coalescence gradually diminish and disappear after several minutes. If the spore wall is cracked gently so as to retain the bubble within the spore, the bubble disappears rather rapidly *in situ.*

Some spore clusters were transferred from SMF to mineral oil and ma-

chine oil, respectively, and when the bubbles were pressed out of these spores thy behaved in much the same manner as in SMF.

If pressure is applied to the spores in SMF in such a way as to temporarily compress but not crack the walls, the bubbles disappear but do not pass out of the spores. When the pressure is suddenly released the

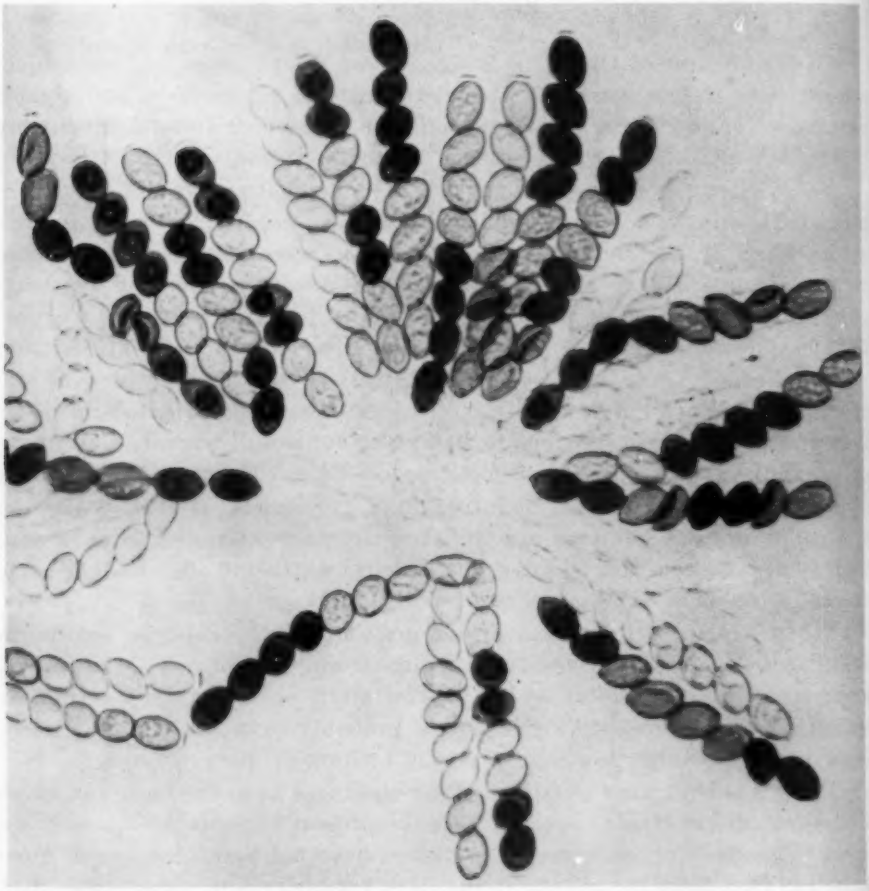

FIG. 1. Hybrid asci from cross of gray-spored mutant with wild-type after transfer to Shear's Mounting Fluid. Note collapsed walls of gray spores and de Bary bubbles in wild-type spores.

spore walls quickly expand back to their normal position and the bubble in each spore simultaneously reappears. Therefore, in view of the collapsing of the gray spores and the behavior of the bubbles within the wild-type spores, it would appear that SMF (or air-drying) causes a rapid extraction of water from the spores, tending to create a vacuum, and that the de Bary

bubbles probably represent partial vacuums containing expanded gases. C. T. Ingold (1956) has suggested that the gas may be water vapor. I should think that other gases, particularly carbon dioxide, might also be present. However, it is not within the scope of this brief study to make a detailed analysis of the composition of de Bary bubbles.

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HISTOLOGICAL RESPONSES OF SOYBEAN SEEDLINGS AND MORPHOLOGICAL CHANGES OF MITOCHONDRIA FOLLOWING TREATMENT WITH TRIETHYLAMINE 2,4,5-TRICHLOROPHENOXYACETATE

C. N. SUN

An atypical growth of soybean seedlings induced by 2, 4-dichlorophenoxyacetic acid was reported previously (Sun 1955 a, 1956). The present study grew out of an interest in the comparison of the way in which 2, 4-dichlorophenoxyacetic acid and triethylamine 2, 4, 5-trichlorophenoxyacetate influence the growth pattern of soybean seedlings. The observation by Fogelberg, Struckmeyer and Roberts (1957), that 2, 4-D and various tumor inducing chemicals cause abnormal proliferation of the cells and also change the form of mitochondria appeared to be particularly significant. In the present study an attempt is made to elucidate further the structure of these mitochondria by the use of thin sectioning procedures in conjunction with electron microscopy.

Materials and methods. Seedlings of the soybean, *Glycine max* (L.) Merrill, 10–12 mm. long, were used for these experiments. Soybean seeds were soaked for 24 hours and germinated on moist filter paper in Petri dishes. The seedlings were first treated in a high concentration of triethylamine 2, 4, 5-trichlorophenoxyacetate (2.4 g./l.) for ten minutes. They were then washed with tap water and cultured in Petri dishes. During the course of the experiment they were rinsed daily with tap water.

The seedlings were examined at various stages after treatment. In the histological studies the same essential techniques for fixation and staining were used as in the earlier experiments (Sun 1955 b). For electron microscope studies, tissues were fixed in buffered osmic acid (pH 7.6) for one hour. After washing, the tissues were transferred to the different solutions prescribed in Walter's technique (1957). After dehydration, they were embedded in methacrylate (butyl and methyl 6 : 1). Sections were cut with the Portor Blum microtome and examined under an RCA EMU electron microscope.

Results. Gross responses. Certain morphological abnormalities were caused in soybean seedlings as a result of the 2, 4, 5-T treatment. Because of the very high concentration of the 2, 4, 5-T (2.4 g./l.) the growth of the shoots was almost completely inhibited. The seedlings, in general, were yellowish green in appearance, and the cotyledons were considerably enlarged. There was also a retardation in elongation of the hypocotyl region and primary root, and a resultant great increase in the diameter of both.

These results are observable on the 6th day after treatment. However, there is no indication of the four-winged broad shoulders on the root and hypocotyl as in the 2, 4-D treated plants.

Histological responses. No definite histological responses were noticed for approximately 12 hrs. following treatment with 2, 4, 5-T. The earliest response was an increase in cell division in the hypocotyl region in the pericycle and pith. This could be observed 18 hrs. after treatment. However, the greatest and most prolonged meristematic activity in the hypocotyl occurred later. This proliferation frequently extended from pith to inner cortical parenchyma. Similar activity was observed in tumors induced by 2, 4-D. Derivatives of cortical parenchyma, endodermis, phloem parenchyma and cambium all showed the dense cytoplasm and large nuclei of dividing cells.

A broad and continuous band of active tissue was formed around the circumference of the hypocotyl inward to the center of the pith. The pith cells of the hypocotyl region became very actively meristematic on the 6th day after treatment. This activity involved the entire hypocotyl region from the periphery to the center. The direction of the effect was centripetal and acropetal (figs. 2 and 3). Because of the proliferation of cambium, phloem and xylem parenchyma, the vascular tissue was less differentiated in comparison with the tissue of a non-treated plant (fig. 1).

The cells of the stele and inner cortical parenchyma became meristematic. As a result of the fact that the inner tissues increased in volume, while the cells in the outer cortex remained almost the same, the outer cortex usually ruptured within several days after treatment. Along the crushed edges, the cells usually lost their polyhedral shapes and became rounded or elongated.

The gross and the histological responses of the root to the treatment with 2, 4, 5-T were similar to those induced by 2, 4-D, but increase in length was less inhibited and proliferation delayed after treatment with 2, 4, 5-T. In the 2, 4-D treated plants, there was a remarkable change in the histological structure of the primary root 3 days after treatment, while corresponding changes appeared in the root of 2, 4, 5-T treated plants only on the 6th day after treatment.

Morphological changes of mitochondria. Studies on the untreated plant have shown that the mitochondria of the soybean cell differ in structure from those of the higher animals. The outer wall of the soybean mitochondria is bounded by a smooth membrane. However, the inner membrane with its internal folds are not lined up perpendicular to the long axis of mitochondria as most mitochondria of higher animals. The haphazard arrangement of the folds in the interior possess minute tubules or villi (figs. 5 and 6) which are similar to those reported in *Paramecium* (Powers, Ehret, Roth and Minick 1956) and *Amoeba* (Cohen 1957). In the

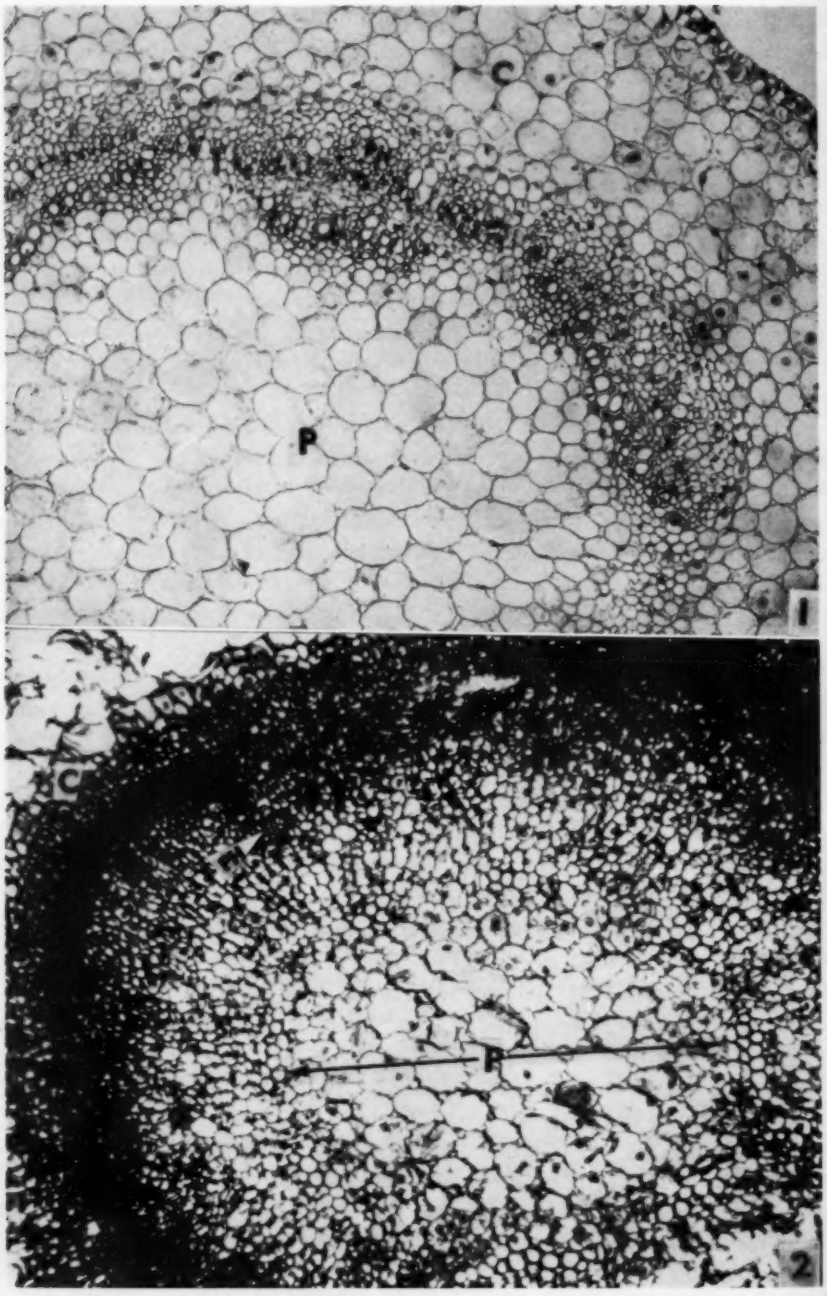
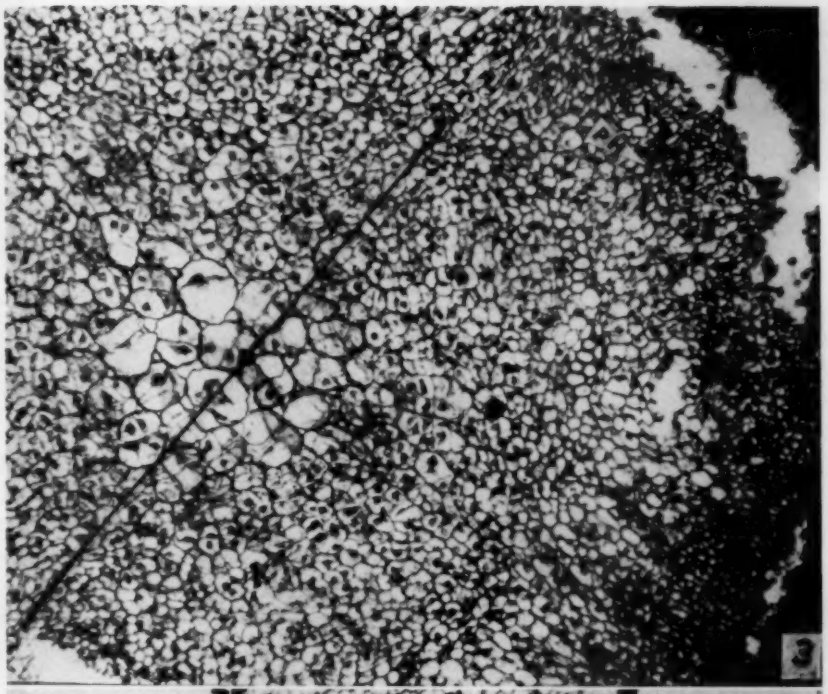


FIG. 1. Transverse section of the hypocotyl region of a 6-day old soybean seedling. *C*, cortical parenchyma; *P*, pith; *Ph*, phloem; *X*, xylem. Magnification × 100. FIG. 2. Transverse section at the root end of the hypocotyl showing proliferation in the inner cortex, vascular tissues and the peripheral region of the pith 6 days after treatment with 2, 4, 5-T. The outer cortex was collapsed. *C*, cortex; *P*, pith; *Ph*, phloem; *X*, xylem; Magnification × 100.



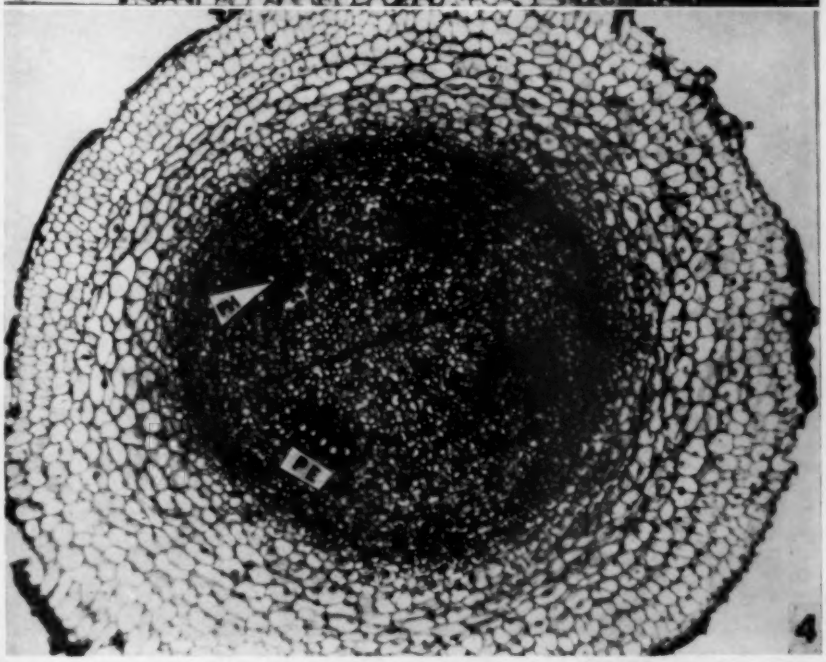
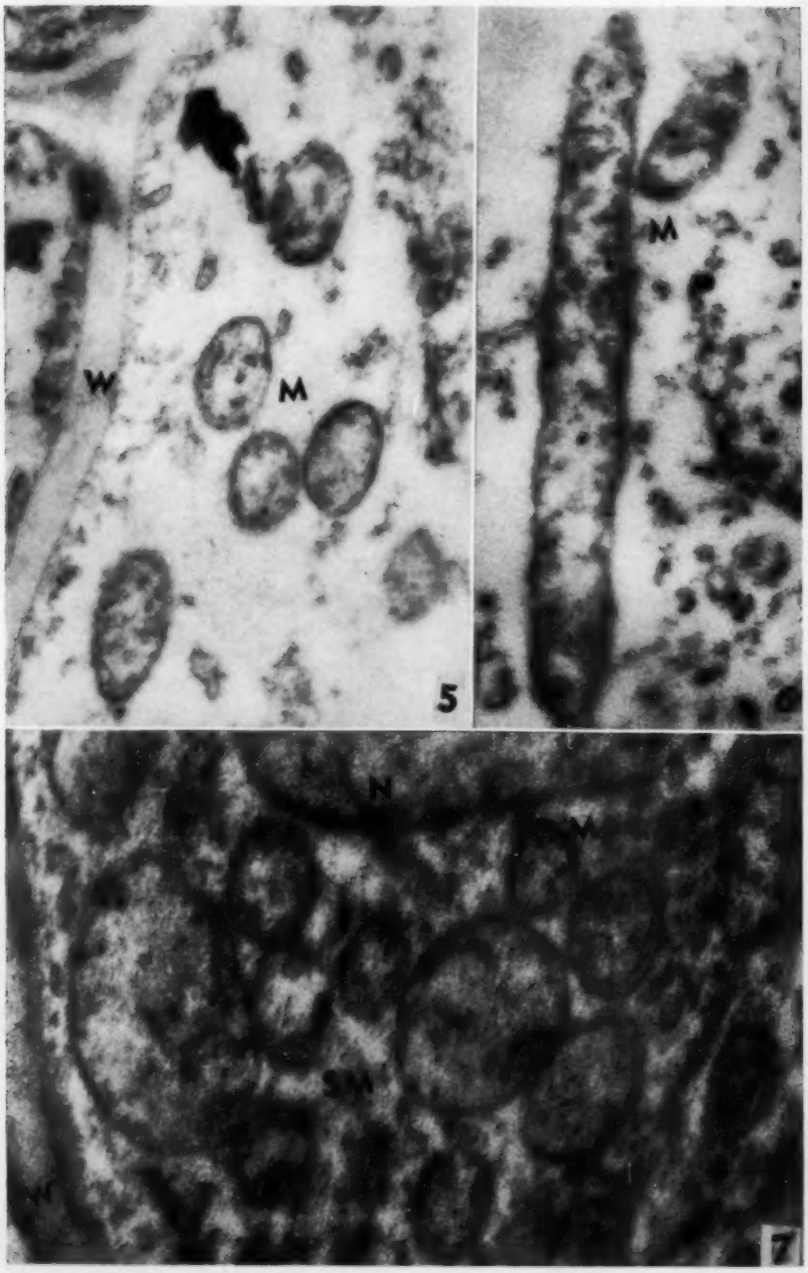


FIG. 3. Transverse section at the upper end of the hypocotyl, showing proliferation 6 days after treatment with 2, 4, 5-T. The direction of proliferation is toward the center. *P*, pith; *Ph*, phloem; *X*, xylem. Magnification × 100. FIG. 4. Transverse section of soybean primary root 6 days after treatment with 2, 4, 5-T. Transverse section taken 1050 μ behind the stelar initials, showing proliferation of inner cortex, endodermis, pericycle and primary xylem. *C*, cortex; *Ph*, phloem; *Pe*, pericycle; *X*, xylem. Magnification × 100.



FIGS. 5 and 6. Sections of mitochondria from the cortical parenchyma cells of the primary roots of soybean showing the mitochondria consisting of minute tubules or villi. *M*, mitochondrion; *W*, cell wall. Magnification × 20000. FIG. 7. Section through a cortical parenchyma cell of 2, 4, 5-T treated primary root of soybean showing the swollen mitochondria. *M*, mitochondrion; *N*, nucleus; *SW*, swollen mitochondria; *W*, cell wall. Magnification × 20000.

cells of the 2, 4, 5-T treated plants, deformation of mitochondria had taken place within 3 days after treatment. The internal membranes pulled apart leaving a more or less extensive central space between them. In some of the cells, the mitochondria appeared swollen and enlarged in diameter (fig. 7).

Discussion. From the standpoint of histological responses, the effect of 2, 4-D of soybean seedlings in many respects paralleled the effect of 2, 4, 5-T. Thus in both treatments, roots and hypocotyl were shorter and larger in diameter than in untreated plants, and there was a similar proliferation in roots and meristematic activity in the pith of the hypocotyl region. There were major differences, however. The most remarkable effect of 2, 4-D was the production of the four winged shoulders in the hypocotyl region and primary root; such shoulders were not induced by 2, 4, 5-T. Vascular bundles and isolated tracheids were differentiated in the meristematic pith tissue as a result of treatment with 2, 4-D, while such differentiation did not occur in the pith of 2, 4, 5-T treated plants.

The mitochondria are important centers of enzymatic activity in the cells (DuBuy, Woods and Lackey 1950, Millerd and Bonner 1953). The morphological changes in the mitochondria induced by treatment with 2, 4, 5-T may have some bearing on the role of disruption of the orderly metabolic and physiological processes and consequently lead to an abnormal growth pattern. However, there is one debatable point, namely, whether changes in the form of mitochondria represent alterations caused by physiological activity or injury referable to abnormal environmental conditions.

SUMMARY

1. Seedlings of soybean, *Glycine max* (L.) Merrill were used for these experiments. Certain morphological abnormalities were caused by application of a very high concentration of 2, 4, 5-T. After treatment, the seedlings showed: enlargement of the cotyledons; retardation in elongation and increase in diameter of the hypocotyl and primary root.

2. Histologically, the earliest response was increasing cell division in the hypocotyl region in the pericycle and pith. Later, the proliferation frequently extended from pith to the inner cortical parenchyma. The pith cells of the hypocotyl region became very actively meristematic. In the root, the cells of the pericycle, endodermis, and inner cortex showed divisions. Pericycle cells were especially active, producing a meristematic zone.

3. Some of the mitochondria appeared swollen and the inner membranes pulled apart. The deformation of mitochondria had taken place within 3 days after treatment.

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TORREYA

The Spotted Violet of High Tor

JOSEPH MONACHINO

On April 22, 1945, and again on May 11, 1958, I collected an acaulescent blue violet with the corolla conspicuously spotted or mottled, irregularly streaked and blotched with white. The recent collection was made into an herbarium specimen and deposited in The New York Botanical Garden (*Monachino 620*, Mount Ivy—High Tor trail, Palisades Interstate Park, Rockland Co., New York State). The leaves of this specimen vary from essentially glabrous to manifestly hirtellous. They are slightly purple-tinted beneath. All the five petals are strikingly violet-white variegated. With its gay dappling, this spotted violet is curiously attractive enough for a garden subject. In my observation both in 1945 and in 1958, the mottled violet constituted a distinct population of many individuals, intermixed with plants of the usual violet corolla type but without any transitional color forms. *Monachino 620* was shown to E. J. Alexander who suggested its specific identity as *V. sororia* Willd., a form atypically glabrescent. He recalled having previously seen mottled flowers of this species and also of *V. triloba* Schw. One plant of the typical form which had grown together with the maculate No. *620* was sent to Norman H. Russell who wrote (July, 1958): "This may be *V. sororia* Willd. but I cannot be sure without more material. The pubescence of this specimen is more characteristic of *V. nephrophylla* Greene".

Because of his interest in the Rockland Co. flora, I informed J. Harry Lehr, in March 12, 1957, of the High Tor station for the spotted violet I had discovered a dozen years ago, and I suggested that he collect living material for pot culture as well as herbarium specimens should he relocate the plant. On the following month, April 28, Lehr explored the Ridge Trail leading to Low and High Tors and found many individuals of a maculate violet growing on both sides of the trail for about twenty feet, a short distance west of Low Tor, the typical form growing with them. He collected two each of the maculate and the typical forms for his herbarium, and in addition he collected eight of the maculate and two of the typical which he potted. Unfortunately, however, he lost the potted specimens during the winter.

My original collection prepared in 1945 was probably from a different colony than that of No. *620*, although made in the same general area. As I then had no interest in studying the plant, I sent it to M. L. Fernald, at the Gray Herbarium, and at the time (my letter to Fernald, 5th May, 1945), I suggested that the species might be *V. triloba*; that it was rather abundant for a distance of at least thirty to forty feet and grew together with the typical form (which I also sent as a sample); and that *V. fimbriatula* Sm. and *V. pubescence* Ait. also grew in the area. J. Harry Lehr informs me that he corresponded with the Gray Herbarium in the attempt to locate the specimen but without success.

Under the title "The Spotted Violet", a brief note by Willard N. Clute appeared in 1947 in The American Botanist 53: 11–13. A photograph was presented, much suggesting our plant. Clute identified his spotted violet as *V. sororia* and described the color as "streaked with dots and lines of white"; he stated that it represented "perhaps an example of albinism, but in any event, it appears to be increasing and now occupies several acres in a moist grove. Specimens brought into the garden not only appropriate a place on shady lawns but show a tendency to spread to other nearby regions." He did not designate the location of his collection.

Frances Wilson in 1895 (Asa Gray Bull. 3: 14) claimed to have seen *V. cucullata* Ait. with blue flowers striped with white, and one specimen with upper petals blue and lower white. Neither Wilson nor Clute published a name to accommodate their

color forms. There apparently is no published trinomial for the spotted-flowered violet, as there are for white-flowered forms of *V. sororia*, *V. triloba* and other species.

Is there more than one species with mottled flowers at High Tor or elsewhere? The spotted violet appears indeed to be worthy of a formal name. Before forma *maculata* is actually published, however, the species should be definitely ascertained by careful study of the plant at least through its complete growth cycle. This can be best done with living cultivated specimens, and it would be well, in addition, to watch the spotted violet for several generations from seed and attempt, if possible, to resolve its genetic background.

Alfred Gundersen

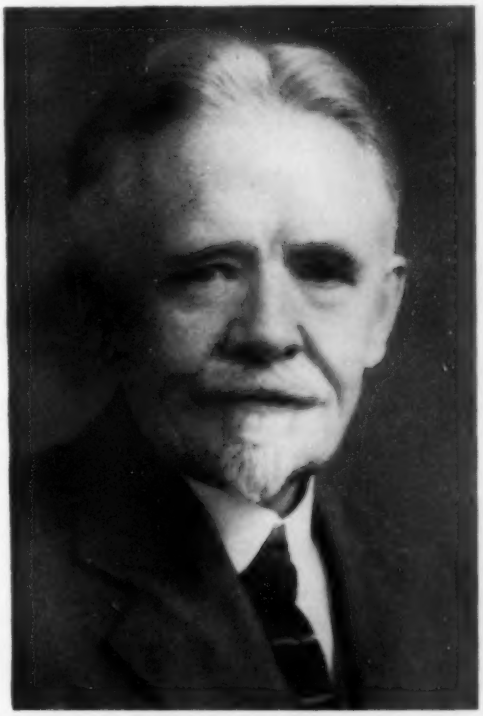
Alfred Ludwig Georg Gundersen was born in Kragerö, Norway, July 1, 1877. He dropped two of these given names in his later life and became simply Alfred Gundersen. His father was engaged in the shipping business and was one of the chief citizens in the little seacoast town in southern Norway on the Skagerrak. Alfred was still young when his father died, and at the age of fourteen came to America to Oregon to join his brother Carl. He also followed his brother to Stanford University and was graduated there in 1897, receiving the degree of B.A. in Physics, and, under David Starr Jordan, becoming interested in evolution problems. He then studied botany for several years under Conway MacMillan at the University of Minnesota, teaching meanwhile in the local public schools. It was here, in Sauk Center, that Sinclair Lewis, one of his pupils, asked his advice about a prospective career as an author, having shown him some of his literary attempts. Gundersen answered with his characteristic "Why not?" Later he studied anthropology at Harvard, receiving the degree of A.M. in 1907. Having decided that he needed still more education, he returned to Europe where he entered the École d'Anthropologie and the Sorbonne, his principal teacher being Professor Gaston Bonnier. He supported himself meanwhile by teaching English in French schools. He once told me that during this period, at the beginning, he attended lectures in French for several months, understanding very little, until suddenly one day, he understood. His ability to speak French with ease stayed with him through life. At length, in 1910, after working at the Laboratoire de Biologie Vegetale, at Fontainebleau, he offered as his thesis, in part, RECHERCHES ANATOMIQUES SUR LES CAPRIFOLIACEES, and received the degree of Docteur de l'Universite de Paris (botany, geology, anthropology).

Returning to America, he obtained a position as Assistant to Alfred Rehder at the Arnold Arboretum, and wrote to his friend of some years back, Miss Mina Westbye, of Trysil, Norway, asking her to meet him in Boston. She looked with favor on this proposal and they met at the steamboat pier in Boston. They were married June 11, 1911, and lived in Boston three years, Dr. Gundersen giving lectures in various Boston institutions in addition to attending to his duties at the Arnold Arboretum. Learning of the new Botanic Garden in Brooklyn, he applied for a position, and was appointed Assistant curator of the Herbarium in 1914, and was gradually advanced, through the years, to a curatorship—Curator of Plants—retiring in 1945 at the age of sixty-eight.

At the Brooklyn Botanic Garden his training peculiarly fitted him to carry on his special work in systematic botany. Indoctrinated early in his career in advanced ideas of organic evolution in his association with David Starr Jordan and others, he applied these principles to the arrangement of the Systematic Section according to the natural or Engler system, which had been adopted at the time of the organization of the Garden. No one could have been better prepared. He was constantly studying the botanic characters of the different families, always with the underlying purpose of determining their rank in the order of evolution. Several articles and maps published in the 30's and 40's reveal the extent of his studies. (3, 5, 7, 8, 9, 11, 12).

During this time other matters in addition to the study of flowering plant evolution occupied his attention. The large collection of *Prunus* at the Garden was the subject of a leaflet (4). The Cycad collection, in the greenhouses, one of the most comprehensive in the United States, was little known and less appreciated. This was described in a leaflet (6) in which I collaborated. Later the growing collection of lilacs at the Garden was carefully described and figured (10).

The interdependence of the plant and animal worlds in organic evolution had always interested Dr. Gundersen, who maintained, and, I believed rightly so, that the subject had been greatly neglected. Briefly, the idea was that the plant and animal worlds in their evolution have been of assistance to each other; that plant evolution, for example, has not progressed by itself alone, but at each stage of advance has derived some support or influence from the animal world. Thus the evolution of the ungulates—horses, cattle, buffalo, etc.—was contemporaneous with that of the grasses. For this group of plants is peculiarly adapted to cropping by such animals, the stem being able to grow again from the nodes if cut off. On their part the ungulates, feeding on the grasses, fertilized them with their dung, and, possessing hoofs instead of claws or toes, were well fitted to travel on the sod of grass land. In a similar way, during the end of the



Alfred Gundersen July 1, 1877—February 21, 1958.

Cretaceous period, the flowering plants developed along with the insects who brought about their cross-pollination, and, at the same time, obtained nectar.

And so, with Mr. G. T. Hastings as collaborator, he wrote an article for THE SCIENTIFIC MONTHLY (13) which concludes as follows: "The spread of flowering plants meant many more insects and more birds. More insects meant more of the small insectivorous mammals. Then came varied groups of larger and specialized mammals, with plant and animal interdependence along new lines, leading up to that between man and food-producing plants. Thus the dependence of the two great worlds of life on each other throws light on successive stages of organic evolution".

Almost from its founding the Brooklyn Botanic Garden had been a participant in what is known as the "international seed exchange". In this way some forty or fifty botanic gardens throughout the world exchange seeds and thereby add to their collections of living and exotic plants—an easy and inexpensive method of acquiring representa-

tive plants of the world. But in the lists of seeds issued by the various gardens each year neither the nomenclature nor the method of listing was uniform. Dr. Gundersen, aided by the director, Dr. C. S. Gager, strove to correct this and obtain a uniform list of names, arranged either alphabetically or according to some agreed system. A great deal of correspondence and much work were involved in this task, and in this connection Gundersen made several trips to Europe, visiting botanic gardens there. In this country the confusion has been greatly cleared up by the publication of STANDARDIZED PLANT NAMES.

Beginning in 1917 he gave outdoor courses at the Garden on trees and flowers, also indoor lectures. These courses were well attended and continued until his retirement.

Gundersen was keenly interested in the Torrey Botanical Club, and rarely missed a meeting. He was a member of the Program Committee from 1921 to 1924, inclusive. As Field Committee Chairman in 1926 and '27 he put new zest into the field trips. For example, at the end of 1927 he reported: "Thirty-five field meetings, with an average attendance of fifteen, were held in 1927. The largest attendance was fifty at the meeting at Staten Island, June 25, led by Drs. Britton and Hollick." (TORREYA **28**: 33. 1928). This was one of our most memorable field meetings, and many of us still remember it with pleasure. Drs. Britton and Hollick, both Staten Islanders, formerly boyhood pals and youthful scientists, were right in their element. In 1928 Dr. Gundersen was followed as chairman by Raymond H. Torrey, who continued the work so well begun, Gundersen remaining as a member of the Field Committee. He was appointed associate editor of the BULLETIN in 1930 and continued in this office until and including 1934. He was elected Vice-president of the Club for 1938, Raymond Torrey being elected President, and at the illness of the latter, which regrettably proved fatal, he assumed the presidency, serving until 1939. The Club scheduled several trips to his summer home in the Catskills, and one year Dr. Gundersen gave a short summer course there, the pupils lodging in nearby boarding houses and with Dr. Gundersen's family.

Soon after Dr. Gundersen came to the Brooklyn Botanic Garden he chose a home at Floral Park, Long Island, commuting to the Garden. During this time a son was born who died while still an infant. It was here also that Sylvia, his eldest daughter was born. Soon afterward the family came back to Brooklyn where Ellen, the second daughter, was born. Mrs. Gundersen writes: "Alfred wanted the children and me to visit Norway so they could learn the Norwegian language (1925–26). That year Alfred visited the botanic gardens in Europe, including Russia".[1] On their return he bought a home in Saugerties, New York, where the two daughters, who are both college graduates, finished their secondary schooling. Saugerties, on the Hudson, was selected because it is only 28 miles from the Catskill summer home of the Gundersens. For, as early as 1919, through Mr. Louis Buhle, a member of the staff of the Garden, Dr. Gundersen became interested in a summer home in the Catskills, and bought more than 150 acres in what was then called "Big Hollow", now Maple Crest. This is in the heart of the Catskills and especially appealed to Gundersen because in some respects it resembled his beloved native Norway. High up in the Catskills in a cove ending in lofty mountains and accessible only by a single road with no other way out or in, the snow lingers for a long time in the spring. He used to visit this place, journeying from the Garden on weekends in fall or spring (before he took the Saugerties home) walking the entire distance from Saugerties through woods and through "Joe's Notch", arriving at his place via the "chalazal" end, so to speak. He loved this mountain home and longed to spend all his time there. His ashes are buried there with those of his little boy, his sister, his brother, i.e., Professor Carl, and the professor's wife.

Alfred Gundersen was a gentleman in every sense of the word, except the connotation that a gentleman does no work. On the contrary, he was most industrious, and, moreover, not afraid of manual labor as his well-appointed mountain home and garden clearly testify. He was never aggressive; also he was always cautious in his scientific writings

[1] See also: Report on a trip to England and Northern Europe. BROOKLYN BOT. GARD. RECORD 20: 25–32. 1931.

about making statements that might be questioned—in fact, I have sometimes thought somewhat over-cautious. I have in mind his excellent book "Families of Dicotyledons" (14), illustrated with careful drawings by the noted botanical artist, Maud H. Purdy. This shows the results of long years of original work, especially along the line of dissection of flower buds (8) bringing out the truth of the well-known dictum "The ontogeny is a recapitulation of the phylogeny," the bud stages clearly showing in many cases ancestral characters. In his introduction he modestly claims no especial credit for these findings, but merely says "the drawings often show differences between flower buds and adult flowers, suggestive of phylogenetic trends."

He was always extremely kind, courteous and sympathetic—qualities which naturally endeared him to his pupils at the Garden. During a large part of his later life he was a vegetarian, and this diet was adopted, I am told, from his revulsion against the idea of killing animals. I have never known him to be angry—only, at times, disturbed when things went wrong. He was, as would be expected from his training, inclined toward a Unitarian belief in religion. Above all, he was a thinker, and interested in many things besides his beloved plants. Among these was the revision of the calendar, and for a time he was also much occupied with a universal language. His scientific interest in the stars was second only to his interest in plants, and he had a speaking acquaintance with all the big constellations. He rarely missed a meeting of the astronomy section of the Brooklyn Institute. At the time of his death he had just completed a primer of astronomy, designed to make clear and simple the main facts about the stars. After finishing this little book he quietly and peacefully passed away at Venice, Florida, February 21, 1958, in his eighty-first year. He was primarily, almost instinctively, a teacher—always trying to make things simple and understandable for the layman.—ARTHUR H. GRAVES, Connecticut Agricultural Experiment Station, New Haven.

The following is a selected bibliography of Dr. Gundersen's writings.

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2. The wild flower garden in June. Brooklyn Bot. Gard. Leaflets. Ser. **V.** No. 7. May 31, 1917.
3. The principal groups of fossil plants. Brooklyn Bot. Gard. Leaflets. Ser. **XVIII.** No. 4. May 14, 1930.
4. The genus Prunus (cherries, plums, etc.) in the Brooklyn Botanic Garden. Brooklyn Bot. Gard. Leaflets. Ser. **XX.** No. 4. May 11, 1932.
5. Flower buds and the directions of floral evolution. Torreya **32**: 154–158. Fig. 1–8. 1932.
6. With Arthur H. Graves. The collection of living cycads at the Brooklyn Botanic Garden. Brooklyn Bot. Gard. Leaflets. Ser. **XXII.** No. 1–2. Feb. 28, 1934.
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8. Flower buds and phylogeny of dicotyledons. Bull. Torrey Club **66**: 287–295. Fig. 1–7. 1939.
9. The classification of dicotyledons. Brooklyn Bot. Gard. Record. **29**: 63–75. 2 figs. 1940.
10. Lilacs in the Brooklyn Botanic Garden including the classification, cultivation, pathology. Brooklyn Bot. Gard. Record **30**: 191–224. Fig. 1–14. 1941.
11. Flower structure and the classification of dicotyledons. Brooklyn Bot. Gard. Record **31**: 99–101. 2 figs. 1942.
12. Flower forms and groups of dicotyledons. Bull. Torrey Club **70**: 510–516. Map. 1943.
13. With George T. Hastings. Interdependence in plant and animal evolution. The Scientific Monthly **59**: 63–72. 7 figs. 1944.
14. Families of dicotyledons. 237 p. Chronica Botanica Co. 1950.
15. World families for angiosperms. Bull. Torrey Club **81**: 210–214. 1954.

Additions and Corrections to a Flora of Rockland County, New York.

Further studies both in the herbarium and in the field have given the writer opportunity to make the following additions and corrections to his "Annotated Preliminary Catalogue of the Vascular Flora of Rockland County, New York (See Bull. Torr. Bot. Club, 83: 435–438, 1956; 84: 48–56, 126–134, 206–213, 310–317, 388–392 and 450–452, 1957)". The abbreviations, the references, and the phylogeny of this supplement remain unchanged from the original catalogue.

POLYPODIACEAE

CHEILANTHES LANOSA (Michx.) D. C. Eaton should read C. VESTITA (Spreng.) Sw.

GRAMINEAE

ARRHENATHERUM ELATIUS (L.) Mert. & Koch forma BIARISTATUM (Peterm.) Holmb. Ramapo. (H)

SPARTINA ALTERNIFLORA Loisel. var. PILOSA (Merr.) Fern. The station for this variety is north of the original county report for the species, resulting in a slight northward extension of its range in New York State. Orangetown. (H)

CYPERACEAE

CYPERUS FLAVESCENS L. var. POAEFORMIS (Pursh) Fern. An additional county station discovered at Iona Island, Stony Point township extends the range of this plant in New York State approximately twenty-five miles northward.

*CAREX CRISTATELLA Britt. Crested Sedge. Haverstraw, Ramapo. (H)

*C. CRISTATELLA Britt. forma CATELLIFORMIS (Farw.) Fern. This station is at the edge of a brackish water inlet subject to tidal influence and the base of the plants are under water at high tide. Haverstraw. (H)

*C. AMPHIBOLA Steud. var. TURGIDA Fern. (*C. grisea* of most auth., not Wahlenb.) Stony Point. (H)

JUNCACEAE

JUNCUS DEBILIS Gray should read JUNCUS ARTICULATUS L. var. OBTUSATSUS Engelm. In brackish soil, in association with *Carex cristatella* forma *catelliformis* and subject to the same influences as that sedge. Haverstraw. (H)

CRUCIFERAE

ARABIS LYRATA L. Stony Point. (H)

CRASSULACEAE

*SEDUM SARMENTOSUM Bunge. Sedum. An escape from cultivation. Stony Point. (H)

ROSACEAE

AMELANCHIER ARBOREA (Michx. f.) Fern. Downy Serviceberry. Ramapo. (H)

LEGUMINOSAE

*DESMODIUM GLUTINOSUM (Michl.) Wood. Pointed-leaved Tick Trefoil. Ramapo. (H)

*D. MARILANDICUM (L.) DC. Smooth Small-leaved Tick Trefoil. Ramapo. (H)

GERANIACEAE

GERANIUM CAROLINIANUM L. var. CONFERTIFLORUM Fern. Carolina Cranesbill. Clarkestown. (H)

EUPHORBIACEAE

EUPHORBIA SUPINA Raf. Milk-Purslane. Orangetown. (H)

AQUIFOLIACEAE

ILEX VERTICILLATA (L.) Gray var. PADIFOLIA (Willd.) T. & G. Common Winterberry. Ramapo. (H)

GUTTIFERAE

*HYPERICUM BOREALE (Britt.) Bickn. Northern St. John's Wort. Haverstraw. (H)

ONAGRACEAE

EPILOBIUM GLANDULOSUM Lehm. var. ADENOCAULON (Haussk.) Fern. should read var. OCCIDENTALE (Trel.) Fern.

BORAGINACEAE

ECHIUM VULGARE L. forma ROSEUM F. Zimm. Although the entire corolla was rose-colored at anthesis, it reverted to the blueness of the typical species in drying. Orangetown. (H)

LABIATAE

*SATUREJA VULGARIS (L.) Fritsch var. NEOGAEA Fern. Wild Basil. Ramapo, Haverstraw. (H)

SOLANACEAE

*LYCIUM CHINENSE Mill. Chinese Matrimony-Vine. Remaining after cultivation. Clarkestown. (H)

LENTIBULARIACEAE

*UTRICULARIA GIBBA L. Humped Bladderwort. Ramapo. (H)

COMPOSITAE

SOLIDAGO CANADENSIS L. var. HARGERI Fern. Ramapo. (H)

S. RUGOSA Ait. var. VILLOSA (Pursh) Fern. Ramapo. (H)

S. SEMPERVIRENS L. var. MEXICANA (L.) Fern. Orangetown. (H)

HELIANTHUS DECAPETALUS L. The writer has deposited a specimen from Ramapo township bearing whorled leaves. (H)

*COREOPSIS LANCEOLATA L. var. VILLOSA Michx. Lance-leaved Tickseed. An escape from cultivation. Ramapo. (H)

*CENTAUREA JACEA L. Star-Thistle. Ramapo. (H)

LACTUCA CANADENSIS L. should read var. LATIFOLIA Ktze., and not the typical species.

J. HARRY LEHR.
Spring Valley, New York.

FIELD TRIP REPORTS

June 18–20. Field Meeting of the Vermont Botanical Society and Bird Clubs. The members and friends gathered in Colebrook, N.H. on June 18th, in time for supper. On the two early morning Bird Walks the group was delighted to hear and see the Mourning Warbler on its nesting ground. The song of the Rose-breasted Grosbeak, Purple Finch and Warbling Vireo were heard so frequently as to make it easy to learn the distinction.

On June 19th the group drove into Vermont and up along the Canadian Border to Island Pond. Here a northern spruce bog was visited, with the usual northern bog vegetation of Leather-leaf, Creeping Snowberry, Swamp Laurel, and Labrador Tea. The Pink Lady's Slipper seemed to be the only orchid in bloom at the time.

On the way home we encountered a porcupine wandering across the road.

The following day the group made an excursion to the Connecticut Lakes Region. At Second Connecticut Lake a beautiful stand of Rhodora was seen in full bloom. The vegetation seemed to be somewhat more retarded here, the Bunchberry was just coming into flower, painted trillium and spring beauty were still in bloom. Along a woods road

used for lumber operations we saw a swamp full of the northern bog plants: Labrador tea, Rhodora, swamp laurel, leather-leaf, and bog rosemary. In drier situations we encountered the Canada mayflower, twinflower, painted trillium, and false Solomon's seal. However the reason for the trip into this lumbering region, was the finding of the nest of the Arctic Three-toed Woodpecker. When the bird was found, sticking his head out of a hole, he was finally persuaded to put in an appearance by a few gentle taps on the tree. Back at the picnic site the Canada Jays were lapping up the crumbs left over from the picnic. The song of the Winter wren and Philadelphia Vireo completed this never to be forgotten birding trip. The botanists in the meantime had discovered a stand of Braun's Holly Fern, and sighted an Eagle and a Raven.

After this perfect excursion the field meeting came to an end with a business meeting of the two clubs, at which Dr. James Marvin and Miss Marion Smith were voted to continue in office for another year. Attendance 34, Torrey Botanic Club 11. Mathilde P. Weingartner.

FIELD TRIP REPORT

June 21. Brewster, Putnam County, New York. After spending nearly three hours around Brewster exploring along roadsides, open meadows, and brooksides, the party drove to Towners to study the vegetation of the swamp below that small town.

From the standpoint of adding to the list of plants recorded from Putnam County, the trip was a successful one. Not all specimens collected have been verified yet, but at least ten new species were added to the county list. In addition, voucher specimens of nine other species which had previously been observed were collected for the first time. Among the additions to the Putnam County flora are: *Arenaria lateriflora*, *Geum laciniatum* var. *trichocarpum*, *Aegopodium podagraria*, *Veronica anagallisaquatica*, *Galium verum*, *Lolium multiflorum*, and *Iris pseudacoris*. These plants were verified by Joseph Monachino, on the staff of the New York Botanical Garden. Attendance 18. Leader, Karl L. Brooks.

June 22–25. Field Foray with the Northeastern Section of the Botanical Society of America. The members and friends of the Section met at Pennsylvania State University, University Park, Pa. on June 22, 1958. A tea and "Get Acquainted Session" was held at the Extension Conference Center in the evening.

At 9 o'clock the following morning the members met in Buckhout Laboratory prepared for a field trip. We were briefed about the area we were to visit, and facilities for collecting of specimens were made available to the group. We were then escorted to a bus which took us into the region of the Seven Mountains, where we first visited a very beautiful stand of mountain laurel in full bloom. *Rhododendron maximum* was just coming into bloom, and the contrast between the pink buds and the white flowers was striking. Lunch was consumed in a beautiful hemlock forest, with virgin trees which more or less darkened the floor of the woodland, so that few plants except fungi could make headway there. Dr. Ferguson, the mycologist however succeeded in making quite a collection which was later exhibited with labels in Buckhout Laboratory. *Isoetes englemani* was collected in a stream. In the afternoon the bus took us to a valley cut into limestone rock by a stream. Here we saw the regular limestone vegetation, particularly ferns and mosses. The walking fern, bladder fern, smooth woodsia were growing on the rocks, and along the road we found bladder-nut, snowberry (*Symphoricarpus racemosus*) columbine (one was 4 ft. tall), teasel, burr oak, canary reed grass, ash-leafed maple, fragrant sumach, carolina geranium, prickly ash and Virginia anemone were growing lustily in this valley.

Supper was a wienie roast on the campus picnic ground, where a red-headed woodpecker put in a appearance.

On June 24th the bus took the group to an abandoned open strip mine near Clearfield, Pa. Here the members became very enthusiastic, collecting many fossils of the carboniferous era (Pennsylvania, 250 million years ago). The *Calamites* seed and tree ferns along with *Lepidodendrons* made up the bulk of the vegetation in those long-ago days. After everybody had collected as much as they could carry, the bus brought us back to an area called the Barrens, where Andrew Carnegie got his start in iron mining.

This area is located on a hill top, and due to a very sandy and sterile soil, as well as very late frosts and terrific heats in the summer the vegetation is very stunted. The scrub oaks had barely begun to leaf out, while others had been killed back by frost. Some of the lower plants were just beginning to bloom. In this barren area a timber rattlesnake slithered across the road, bringing the bus to an abrupt halt. We were all glad we were in the bus, and we stayed there.

There being no evening program, some of the members toured the Botany Laboratories, while others toured the beautiful campus of the University, a veritable Arboretum. There were: Kentucky coffee tree, cucumber magnolia, yellow-wood, Ginkgo, Japanese dogwood, Japanese lilac, and many other trees and shrubs, all gorgeous specimens.

On June 25th, we again went by bus to a swamp called Bear Meadow. Some of the hardier members went bog-slogging, finding sundew, poison sumach, fruiting *Sphagnum*, withe-rod, *Carex foliculata*, and the Massachusetts or bog fern. Those members preferring higher ground followed a trail along the meadow edge and found many fungi, red-berried elder, mountain laurel, azalea and other woodland plants of the mature forest.

At the business meeting plans were made for a meeting (business) at the University of Massachusetts next year, just prior to the Botanical Congress, which will be held in Montreal in August.

Dr. Theodore Koslowski was elected Chairman, Dr. John Small Vice-chairman and Dr. William Niering Secretary-Treasurer. Attendance 42. Torrey Botanical Club 12. Mathilde P. Weingartner.

Book Reviews

Carl Linnaeus, Species Plantarum. A facsimile of the first edition, 1753. Volume I, with an introduction by W. T. Stearn. London: printed for the Ray Society. 1957. £2.10 [$7.00.]

One of the remarkable things about Linnaeus is that his entire system was conceived in his youth. The *Systema* appeared in 1735, the *Genera* in 1737, the *Classes* in 1738. While he was thus disposing of the larger elements, he was attacking species also: the *Flora lapponica* saw the light in 1737, the *Hortus cliffortianus* in 1738. During the same period he was concocting a vast analytic plan for the organization of the plant kingdom, and providing the objective data to be thus organized. The *Species plantarum* of 1753 was the crown of the plan; but the task was outlined as early as 1733. The value of the work is, of course, not due solely to its antiquity and rarity. It is the official beginning of botanical nomenclature, and in a sense the beginning of botanical taxonomy too, since it provides the first really useful descriptions of species on an extended scale.

Since copies of the original edition are readily accessible only to a few, the usefulness of a reprint is obvious. We have already had one, a facsimile published in Tokyo about 1935. (Such editorial comments as were provided were unfortunately in Japanese.) Now the Ray Society has prepared a second facsimile, of which the first volume is at hand. It is a neat book, with a frontispiece in color showing the famous Wedgwood medallion of Linnaeus; and, much more important, with an extended "introduction" by an eminent botanical bibliographer. (I recently saw, in South Kensington, the page proofs of the second volume, which will include appendices from the same hand.)

With a probably unequaled knowledge of botanical literature and with the splendid resources of the library of the British Museum (Natural History) at hand, William Thomas Stearn has provided not merely an introduction to the *Species plantarum* but a discourse on the method and philosophy of Linnaeus that can well stand by itself as a basic tool in plant taxonomy. Much has been written, of course, on Linnaeus and on the *Species;* in fact a vast and scattered literature in many languages has grown up; this is here skillfully digested and concisely presented, with much additional information. While part of this matter is familiar to every experienced taxonomist, much of it will be new to at least the great majority (including the present reviewer).

A preface explains the connection with John Ray, whose greatness Linnaeus appreciated and acknowledged. I have often wondered if a "natural" classification based

on Ray's genius would have prevailed earlier if the "sexual system" of Linnaeus had not been so easy to use. Is it possible that Linnaeus retarded the development of classification as we know it today? Probably not—the need of the time was for a simple system to resolve the current chaos. In Chapter IX Stearn deals with the reception of Linnaeus' system in England (one is left to wonder about its influence on botanists of other countries—but the English are like that!). In his account of John Hill he omits the commonly received story that Hill was knighted by the King of Sweden for his part in introducing Linnaeus into England: though he had no use for an artificial classification, he adopted Linnaean nomenclature and his principles of description.

In Chapter IV the presentation of the "sexual system" is enlivened by quoted comments from the 18th and 19th centuries, which ran to expressions on the "lewd method" and the "loathsome harlotry" that provided several males for one female. Chapter VIII deals in detail with the preparation of the *Species* and the introduction of binomial nomenclature. In Chapter XI we find the older literature used by Linnaeus, and in XII an account of Linnaeus' own herbaria (not all in Burlington House), so important in attempting to typify Linnaean species. Other chapters treat of Linnaeus' life, of his major publications, of the dissertations and their authorship (this seems to wander a bit from the subject, but we are glad of the information), of the various editions of the *Species*. The lists of abbreviations, signs, and place-names used by Linnaeus will certainly be found very useful. There are, of course, numerous references to the literature on the subject, and an index to the whole "introduction." In all it comprises 176 pages—a fair-sized book in itself.

The presentation is systematic, lucid, and eminently usable. There may be errors; if so I do not recognize them. In one small matter I should take issue with Stearn; it concerns Linnaeus' character, not the *Species plantarum*, and is perhaps, after all, largely a question of language. It seems to me that he overemphasizes Linnaeus' objectiveness at the expense of his imaginative and reflective powers. Linnaeus dealt capably with the raw materials of science, which is one of the achievements that makes him still valuable. But—even more important—he formulated the intellectual concepts that underlay his method. His *Philosophia* of 1751 is in fact a philosophy.— H. W. RICKETT.

Drawings of British Plants. Part XI. By Stella Ross-Craig. 39 plates and index. London: G. Bell & Sons, Ltd. 24 Apr 1958. 9/6 [$1.33].

This part includes families from Droseraceae to Ficoideae (in the Bentham and Hooker sequence). The three species of *Drosera* grow also in the United States, as do *Hippuris vulgaris* and two of the three species of *Myriophyllum;* of the six species of *Callitriche* we have two; the three Lythraceae include two lythrums that grow here; in the Onagraceae we find *Ludwigia palustris, Oenothera biennis, Circaea lutetiana, intermedia,* and *alpina,* and 14 species of *Epilobium* of which we have four; the part concludes with two fine plates of *Bryonia dioica,* the only wild cucurbit of the British Isles, and one of *Carpobrotus edulis* (*Mesembryanthemum edule*), the Hottentot fig, which has become naturalized in Britain as in California.

The details shown of flowers and fruit are all one could wish for in identifying these plants or getting to know their morphology. Even the diminutive flowers of *Myriophyllum* and *Callitriche* are clearly represented. Trimorphy in *Lythrum salicaria* is beautifully illustrated (it gets scant mention and no illustration in current manuals and "wildflower books"). And where else can one find enlarged parts of the leaf of *Drosera,* showing the glandular hairs, and of the stipules, gynoecium, and other details?— H. W. RICKETT.

The Mushroom Hunter's Field Guide. By Alexander H. Smith. 197 pages, 138 plates. The University of Michigan Press, Ann Arbor, 1958. $4.95.

This book by the foremost American authority on mushrooms is a valuable addition to the literature on common edible and poisonous mushrooms. While especially designed for those who collect mushrooms for eating, it should prove to be of considerable value

for the amateur mycologist who merely wishes to know the names of common mushrooms. As indicated by the author, the purpose of the book is to serve as a field guide to give mushroom hunters better protection against serious mistakes. The guide is not designed to enable people to make scientifically accurate identifications. Major emphasis is given to the identification, by use of illustrations, of 124 kinds of common mushrooms. Following an introduction, the mushroom as a plant and the parts of the mushroom, with line drawings, are discussed, and general comments and advice with appropriate warnings on poisonous versus edible mushrooms are given.

Identification is accomplished through the use of clear and concise keys and excellent black and white photographs of the species. Under each species considered are comments on when and where to find it, important field characteristics and edibility. The author's comments on edibility provide a wealth of knowledge based primarily upon his own personal experiences and makes the book most valuable to all mushroom hunters. The author uses the term mushroom in the broad sense and includes the true morels (5 species), false morels (4), puffballs and related species (7), hedgehog mushrooms (7), coral mushrooms (5), chanterelles (6), polypores (3), boletes (18) and gill mushrooms (69). Some fifteen edible mushrooms are listed as being safe for beginners. The book will be most useful for those collecting in the northeastern United States, Great Lakes region and the western United States. A list of mushrooms associated with certain trees and a list of selected mushrooms, indicating where they can be found according to season, provide useful aids to the mushroom seeker. A glossary and list of books on mushrooms round out the book.

The book is elongate in shape being 11" × 5¼", apparently the shape to fit in a large pocket of a field jacket. Without question, this is the best of the available books on common edible and poisonous mushrooms.—CLARK T. ROGERSON, New York Botanical Garden.

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LAZELLA SCHWARTEN

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